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Bird talk, the soap opera:
vocal and behavioural repertoire of a zoo population of rainbow lorikeets (*Trichoglossus moluccanus*)

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When I turned 22 I was lucky to start working in the bird show area of the Lisbon Zoo, where I stayed for one and a half years. Overnight I became a caretaker and trainer to dozens of animals of very different species that had ended up on that corner of the park after being rejected by their parents or social group in the zoo's other areas, through being donated by human parents that could no longer assure their care, through being rescued at the Lisbon international airport from illegal smugglers. Every day I heard them communicate with each other, or with seemingly no one, and I talked to them (almost) as much as they talked to me. They were actually my favorite lunch company, and I practiced mimicking their calls all the time. Even if it sounds cliché and cheesy, the truth is each of them had their own way about life, their own recognizable voice and body language, and by interacting with them I learned about myself and how I carry myself in this human life. The energy I emanated had dozens of fuzzy mirrors full of colourful feathers, powerful beaks and sharp claws, and I adapted my emissions to make their life as best as it could be. That was a powerful, life changing lesson.

Birds are funny beings. As well as being beautiful, colourful, fast, agile, loud, quirky, cute, majestic, photogenic, intelligent, social, cuddly, skittish, discrete, omnipresent, picky, mesmerizing, unexpected, free.

This is my love letter to you, in the least most nerdy way possible.

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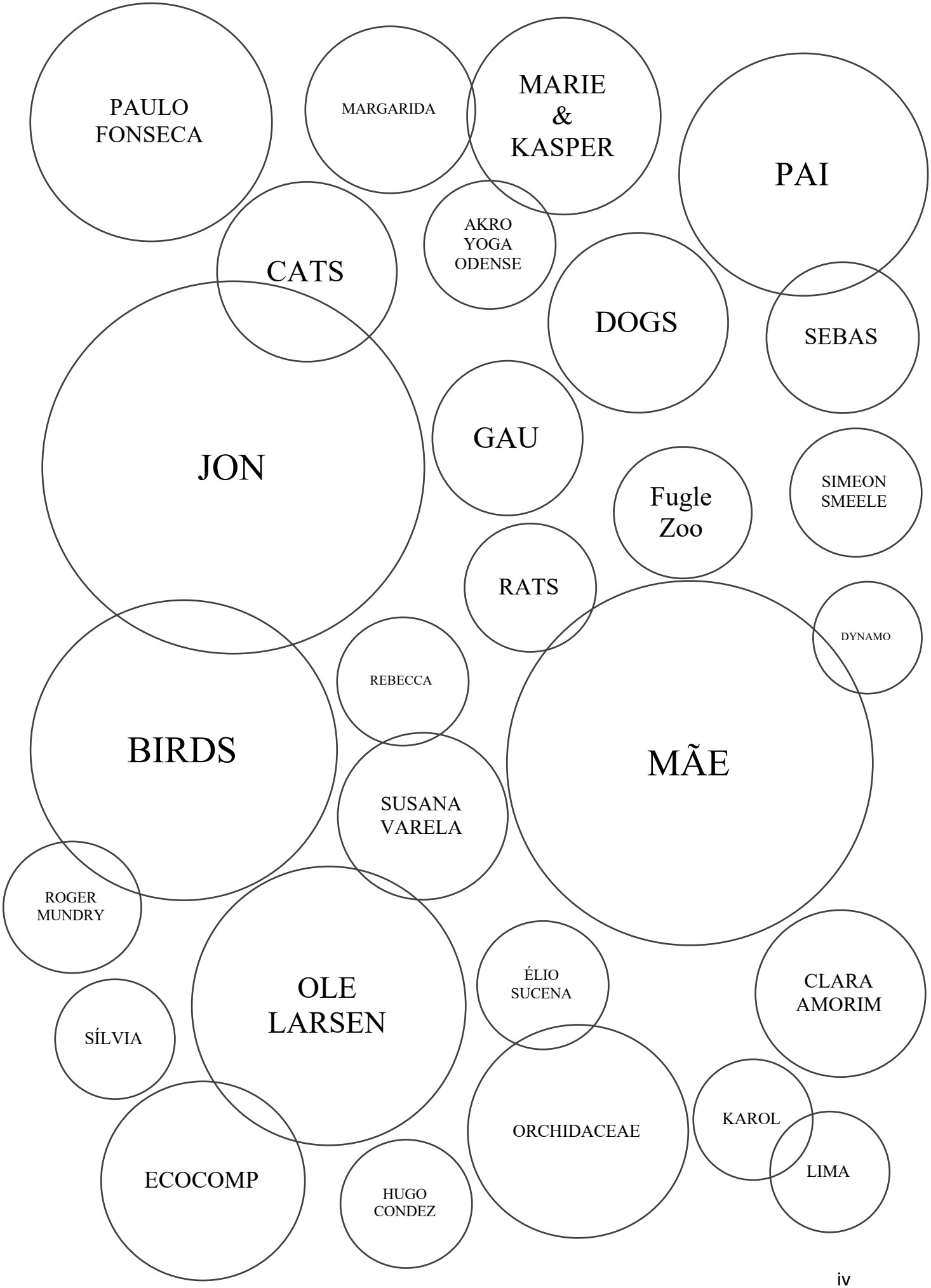
PAULO FONSECA
MARGARIDA
MARIE & KASPER
PAI
AKRO YOGA ODENSE
CATS
DOGS
SEBAS
JON
GAU
Fugle Zoo
SIMEON SMEELE
RATS
DYNAMO
REBECCA
BIRDS
MÃE
SUSANA VARELA
ROGER MUNDRY
ÉLIO SUCENA
CLARA AMORIM
OLE LARSEN
SÍLVIA
KAROL
ORCHIDACEAE
LIMA
ECOCOMP
HUGO CONDEZ

And to all the kind souls that (maybe unknowingly) supported my sometimes-demoralized self by saying “wow that’s so cool” when I described what I was doing for a master’s thesis.

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ABSTRACT
(English)

Psittaciformes, or parrots, are universally and historically recognized not only for their innate vocalizations and mimicry skills, but also for their cognitive skills, compared to the ones of primates. The origin of these two features is still discussed, many times symbiotically, on various biological and scientific levels. The two main evolutionary hypotheses that explain these – the social brain hypothesis and the relationship intelligence hypothesis – greatly draw on the complex social structure, predominance of monogamy and daily foraging variety of these birds as a basis for the appearance of these attributes. Psittaciformes are, furthermore, of interest on the research of the evolution of language, since they too exhibit cultural drift from flow of individuals between populations, resulting in dialects in the vocalization repertoires. Parrots are, however, not very well studied in relation to their worldwide fame. They are common exotic pets whose wild populations are under threat due to long-lasting intense trading market, and at the same time have become invaders of new environments by escaping or being deliberately released.

My aim was to describe the vocal and behavioural repertoires of a previously less-know Australian parrot, *Trichoglossus moluccanus,* or rainbow lorikeets, and correlate these with hypotheses on vocal learning and evolution of cognition. Through a descriptive study complete by and acoustical approach, these birds showed complex group dynamics between the 11 analysed individuals and evidence of a possible convergence of vocalizations within the group. Their behavioural and vocal repertoire here described are the most complete on this species so far, including 45 behaviours and the acoustic characteristics of 12 call types, with respective contextual association between the two. One fully recorded mating event, unprecedented in rainbow lorikeets, is described in detail.

These features make this species one of good value for research on both its healthy wild and captive populations, on themes such as parrot ecology, the influence of the human presence on their behaviour, the evolution of dialects and ritualized behaviours from cultural differentiation, vocal learning and mimicry, and the evolution of non-primate and general cognition, intelligence and language. Findings on species such as these could help improve conservation efforts to similar endangered species, through the increase of knowledge on this taxonomic group, while calling attention to the importance of cultural assimilation in programs for reintroduction.

KEYWORDS

vocal learning and mimicry, parrots and psittaciforms, rainbow lorikeet, invasive species, evolution of language and dialects, behavioural and vocal repertoires, evolution of cognition, social brain hypothesis, relationship intelligence hypothesis

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RESUMO
(Português)

Se a comunicação é a base de todas as interações e relações sociais, a comunicação acústica é uma das mais predominantes. Esta forma de transmissão e receção de sinais é muito variada e existe praticamente em todos os animais, mas há certamente alguns que se destacam. Os psitaciformes – ordem que inclui papagaios, araras, catatuas, periquitos, entre outros – são universalmente e historicamente reconhecidos não só pelas suas vocalizações inatas e aptidões de mímica, mas também pelas suas capacidades cognitivas, comparadas às dos primatas. A origem destas duas características ainda é discutida a nível evolutivo, neurobiológico, ecológico, fisiológico, comportamental e acústico. As principais hipóteses evolutivas que as procuram explicar – a *social brain hypothesis* e a *relationship intelligence hypothesis* (hipótese de cérebro social e hipótese de inteligência relacional) – baseiam-se muito na complexa estrutura social, na predominância de monogamia e na variação diária de estratégias de alimentação destas aves para o aparecimento destes atributos. Além do mais, os psitaciformes são de grande interesse para a investigação sobre a evolução da linguagem, visto exibirem deriva cultural devido a migração de indivíduos entre populações, resultando em dialetos nos reportórios vocais.

Contudo, os psitaciformes estão ainda pouco estudados, sobretudo comparando com a sua fama mundial como mímicos e aves decorativas. São animais de estimação exóticos comuns cujas populações selvagens estão sob pressão devido ao tráfico internacional de longa data, e que, ao mesmo tempo, se tornaram invasores de ambientes diferentes do seu por escaparem de cativeiro ou por serem libertados intencionalmente. Graças a estas duas condições, estão em ação programas de conservação para aumentar os números das populações naturais de várias espécies deste grupo taxonómico em perigo, enquanto elementos de outras espécies se tornaram vizinhos numerosos e inesperados em áreas humanizadas.

Propus-me a descrever os reportórios vocal e comportamental numa espécie australiana pouco conhecida de psitaciformes, os *rainbow lorikeets* (*Trichoglossus moluccanus*) ou lórios-arco-íris, e correlacioná-los com hipóteses de aprendizagem vocal e evolução de cognição. Esta espécie invasora exibe interações sociais complexas, neofilia e bioacústica diversa e ainda por estudar. Este objetivo foi conseguido através de observações e gravações de comportamento e vocalizações, durante várias semanas, e foram feitas análises estatísticas e acústicas usando espectrogramas e 20 parâmetros acústicos selecionados. Estas revelaram uma dinâmica de grupo complexa entre os 11 indivíduos analisados, com sinais de hierarquia independente do sexo através de interações agonísticas e o casal como a unidade social do grupo. Os seus reportórios comportamental e vocal aqui apresentados são os mais completos nesta espécie até agora, incluindo descrições de 45 comportamentos discretos e as características acústicas de 12 tipos de vocalizações distintos, com a respetiva associação contextual entre os dois repertórios. Um evento de acasalamento completamente registado, sem precedentes em lórios arco-íris, é descrito em detalhe do início ao fim. Adicionalmente, há indícios de uma possível convergência das vocalizações dentro do grupo, devido à falta de diferenças acústicas significativas entre as vocalizações dos indivíduos ou entre as dos dois sexos, o que poderia indicar uma adaptação de indivíduos de origens diferentes origens à vida num grupo fechado ao longo dos últimos anos.

Grupos numerosos de *Trichoglossus moluccanus* têm surgido em algumas das maiores cidades da Austrália, uma mostra do forte poder adaptativo destes psitaciformes de comportamento complexo e capacidades vocais dinâmicas. Analisadas através de um estudo descritivo, algo raramente observado hoje em dia, estas características fazem desta espécie uma mais-valia na investigação tanto de populações selvagens como em cativeiro, em temas como a ecologia de psitaciformes, a influência da presença humana no seu comportamento, a evolução de dialetos e comportamentos ritualizados devido a diferenciação cultural, as capacidades de aprendizagem e mímica vocal, e por fim a evolução da cognição, inteligência e linguagem em geral e em não-primatas. Em simultâneo, descobertas em espécies como estas podem ajudar a melhorar esforços de conservação em espécies semelhantes em

vias de extinção, ao aumentar o conhecimento sobre Psittaciformes e ao realçar a importância da assimilação cultural em programas de reintrodução.

PALAVRAS-CHAVE

Palavras-chave: aprendizagem e mímica vocal, psitaciformes, lório arco-íris, espécies invasoras, evolução da linguagem e dialetos, reportórios comportamental e vocal, evolução da cognição, social brain hypothesis, relationship intelligence hypothesis

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LIST OF ABREVIATIONS

Dim – Dimension of the Principal Components Analysis

IUCN – International Union for Conservation of Nature

F – female

GLMM – Generalized Linear Mixed Models

IQR – the interquartile range of frequency values, that is, Q75-Q25

KW – Kruskal-Wallis

M – male

MW – Mann-Whitney

PC – Principal Component

PCA – Principal Components Analysis

pDFA – permuted Discriminant Function Analysis

Q25 – the first quartile of frequency values

Q75 – the thirds quartile of frequency values

SDU – Syddansk Universitet – University of Southern Denmark

SEM – standard error of frequency mean

St. residuals – standard residuals of the Pearson's chi-squared test

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INTRODUCTION

1.1 Acoustic communication

Communication is the basis upon which all interactions and social relationships form and develop (Brumm & Slabbekoorn 2005). A very common type is acoustic communication, a form of sending information by encoding a signal and transmitting it from sender to receiver through the means of sound (Shapiro 2010). Animal communication signals have a range of acoustic variations, including both discrete and continuous variants (such as number of calls and length of calls, respectively), and call combinations. One of the most prominent groups in this study area are birds, for their universally known, and heard, vocalisations and songs.

The acoustic structures of avian vocalisations show a high degree of variation in pitch, duration, signal shape, repetition rate, and several birds combine discrete types of notes or calls into higher complex sequences, forming songs (Sozuki 2016). For the birds capable of vocal learning, namely oscines or songbirds, Psittaciformes – widely called parrots – and hummingbirds, the sound repertoire is acquired throughout the individual's life, in opposition to innate vocalisations with which the individual is born with. The repertoire is built using diverse strategies, with different periods in life for learning, number of songs learned, and higher or lower fidelity in their reproduction (Beecher & Brenowitz 2005). By the definition of learning, this sophisticated communication becomes a skill that can be used during the life of the individual, and if the animal is capable of contextual learning, it will be able to use the learned vocalisation in different contexts from the one that originated the learning process, according to how it sees other individuals using it (Tyack 2008). It may come from the complex social systems that many birds live in, involving cooperators and competitors from the same species or not (Krams et al. 2013), and involves underlying cognitive processes which are amply studied in function and evolution but still not completely understood.

The neural basis for those mechanisms, nevertheless, have been studied for decades and in enough detail to compare with human auditory processing and vocal production. Birds have specialized brain nuclei and neural pathways that mediate vocal learning and the production of learned vocalisations (Jarvis 2004, 2006), and that are absent in birds without vocal learning (Feenders et al. 2008). It is suggested that these neural structures and their connectivity evolved independent in the three avian groups, but arouse from a modified motor system inherited from the shared ancestor (Feenders et al. 2008). This theory can account for the differences existing between parrots, songbirds and hummingbirds in this skill.

1.2 Vocal mimicry

One example of such differences is vocal mimicry, a process in which the production of novel communication signals out of the animal's repertoire is based on sounds that do not come from conspecifics (Petkov & Jarvis 2012). Psittaciformes and some songbirds are prime examples of such skill. There are very few species in the animal kingdom capable of this type of imitation, due not only to neural constrains but also to the need for vocal flexibility, limited by their physiology (Fitch et al. 2010). These vocal abilities are indeed prevalent, and famous, in parrots. It is hard not to associate parrots to their image of funny imitators of human speech, whether on the shoulders of pirates or in countless viral videos.

Neurobiologically, cortical nuclei in parrots consist of two adjacent regions that are both active during the production of learning vocalisations, while songbirds and hummingbirds have only one. Furthermore, one of these vocal nuclei is surrounded by auditory responsive neurons (Jarvis & Mello 2000).

Ecologically, the functionality of most parrots' learned vocalisations is quite different, as they are used in a wide variety of social contexts, are produced by both sexes equally, are expanded through the whole individual's life, and typically leads to large repertoires (Balsby & Bradbury 2016); in fact, much like humans, the most prolific vocal learners and mimics. In contrast, the acquisition of new songs, elements or calls by many songbirds ends at a certain age (Catchpole and Slater 2008), the females of most species have lost the ability to learn song (Price et al. 2009), and 80 percent of songbirds learn a maximum of five songs in their lives (Beecher and Brenowitz 2005). Moreover, while songbirds use their learned songs and calls mainly in the context of sexual selection (Collins 2004), parrots' vocal learning appears to be unrelated to mate attraction, but it is instead linked to nest defense, foraging system and complex social dynamics. (Balsby & Bradbury 2016).

There are, after all, surprising similarities between vocal communication possibilities of parrots and humans, making these birds an arguably acceptable model for the study of the evolution of language and speech, albeit not without constraints (Balsby & Bradbury 2016).

1.3. Evolution of cognition

Parrots' brains are among the largest in the animal kingdom, both in relative brain size (brain to body mass ratio) and relative neocortex size (ratio of the neocortex size to the total brain) (Fig.1.1). In fact, their forebrains and the ones of corvids show the same relative size as those of the great apes, where the focus of intelligence research has been due to their evolutionary proximity to us humans (Emery 2006). Moreover, the cerebrum of parrots, particularly the nidopallium – whose neuronal nuclei have been related to vocal learning – is quite larger than the ones of other species in relation to body size (Iwaniuk et al. 2004). Brain size is usually linked to heightened cognitive abilities, mainly because of the physiological and evolutionary costs of having such an unexpected brain, and is often used as proxy for intelligence (MacLean et al. 2012).

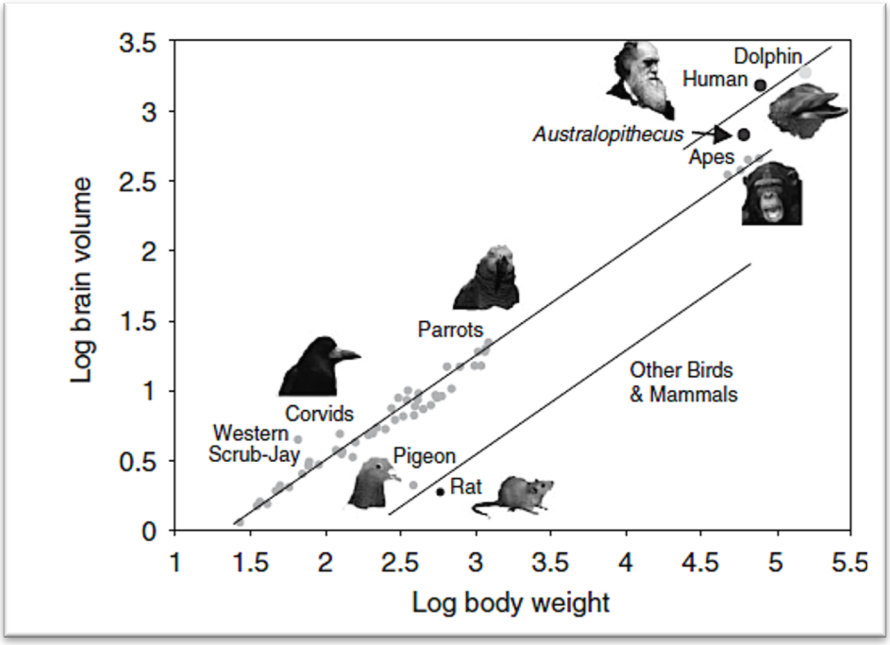

Fig.1.1. Relation between brain volume and body weight for some species of birds and mammals.
From Emery & van Horik (2011) with the following legend: "Relative brain size across birds and mammals. Graph displaying the relationship between (log) body weight and (log) brain volume across various birds and mammals (e.g. corvids, parrots, apes, dolphins, Australopithecus and modern *Homo sapiens*, pigeons, and rats)."

As for how and why these unexpected brain size and cognitive skills evolved – even if it is not only the size of the brain but also its structure and nuclei composition that allow the species to have certain abilities – several hypothesis that attempt to explain it can be directly applicable to the most intelligent birds, such as parrots. Two of them, that are becoming more and more prevalent, correlate to bird's complex social structures.

The social brain hypothesis (Dunbar 1998), suggested by Byrne and Whiten in 1988 with the original name "Machiavellian intelligence hypothesis", relates relative brain size with mechanisms to maintain group cohesion – it emphasizes the role of sociality to solve ecological problems arising from foraging together within a big aggregation of individuals, since each individual must meet their own needs while coordinating their behaviour with the others, also defusing conflicts caused by the cohabitation. At the same time, the choice for a species to live in big groups comes from increased benefits in living gregariously, and refers to novel technical innovation and acquisition of new food sources through social learning as big advantages (Dunbar & Shultz 2007).

While this was mainly explored for primates at first, a complementary hypothesis suggested by Emery et al. in 2007 – the relationship intelligence hypothesis – adds the extremely common long-term monogamous partnerships in birds, such as parrots, as a demand for elaborate socio-cognitive abilities. It suggests that the maintenance of these long pair bonded monogamous relationships requires increased cognitive skills, to ensure a stable and successful partnership with mutual benefits for both individuals, while not excluding the complex social environments in which these relationships arise.

Fittingly, most parrot species show a prevalence of socially monogamous pairs and solitary nesting (Balsby & Bradbury 2016) over other mating systems, which can make this taxon eligible for the relationship intelligence hypothesis. Songbirds express this mating tendency as well, which has been a reason to dismiss the choice of mating system as an explanation for the differences in vocal learning between the two bird taxa. However, since songbirds rely more on male-owned and -defended territories, while parrots organize in a different social structure, it is possible that the action of both the evolutionary hypothesis above potentiated the parrot's cognition and brain size and complexity, allowing for a step further in the development of vocal learning.

The aforementioned social structure is parallel to the dominant monogamous lifestyle: the majority of parrots live most of their lives in very large fission-fusion groups. These numerous flocks can maintain a stable core of individuals but otherwise lose and receive new individuals every day and with every foraging expedition, though pair mates primarily remain together (Balsby & Bradbury 2016). They use soft calls to coordinate foraging within a food patch (Bradbury 2003), and the loud, widely studied contact calls while in flight, in interactions with other flocks or between members of a mating pair when separated (Juniper & Parr 1998). Therefore, vocal and social learning are very much relied on for sharing foraging information throughout the group, since experienced individuals will provide example and callings on where to feed for more naïve ones (Giraldeau & Caraco 2000).

1.4 Dialects

Acoustic communication is also essential for the coexistence of so many individuals, regarding the transmission of information. In parrots, calls can label the individual who produces them on such attributes as identity, provenance or sex (depending on the experience of the receiver). Calls also act as negotiation and mediation between the group's individuals and in establishing relationships of dominance and submission, sometimes serving both purposes (Balsby & Scarl 2008, Buhrman-Deever et al. 2008). In fact, calls have been shown to change according to the identity of the sender and of the receiver, and their relative roles (Wanker et al. 2005). Since calls are commonly used for recognition of

conspecifics, for mate choice and even for the maintenance of social relations, the inability to convey these signals can lead to rejection of newcomers.

An aftereffect of parrot's incredible vocal learning skills and complexity in acoustic communication, as well as their ability for dispersion, is the existence of a cultural drift, also studied in songbirds (Curé et al. 2012). Flocks become populations and populations occupy different geographical areas, and, with a reduced flow between them, dialects are created, comparable to human dialects or languages (Cavalli-Sforza 2000). These can even be maintained with genetic flow between the populations, which is coherent with selection to maintain the skill of vocal learning in the species: whenever new individuals join a group, they must quickly adapt to the pre-existing calls to order to gather useful information and feed successfully, eventually even mate. Vocal matching allows them to do all of the above (Berg et al. 2011, Wright et al. 2005). This process may of course be faster or slower, varying between individuals and across species, depending on mimicry skills (Balsby & Bradbury 2016). Dialects have been described in numerous species of animals capable of learning vocalisations, including parrots, songbirds and hummingbirds, as well as bats and cetaceans (Wright 2017).

It is suggested that while the maintenance of vocal dialects might be due to their role in signaling group membership and familiarity, as well as the aforementioned cultural drift, it might originate and be reinforced by accumulated errors during learning in isolated groups. However, there seems to be no evidence pointing to dialects being a result of genetic differences, merely a parallel phenomenon resulting from the same separation of populations that drove the dialects to form (Wright 2017).

Interestingly, there is strong evidence pointing to parrot nestlings learning their acoustic repertoire from on parental and early life templates from their caretakers, independently of being related to them (Berg et al. 2013). With possible of genetic flow between populations with different dialects, this ability is essential for the young parrots to be integrated in the population they are born in by acquiring its calls, even if their ancestry in another. Even if their caretakers are from another species, such as humans. This imprinting is expected (Chapman & Rowley 1986), considering parrots' high sociability and learning abilities.

1.5 Study species – the rainbow lorikeet

Parrots is the colloquial name for Psittaciformes, a diverse order of birds with hundreds of species, distinct by their strong, curved beak, upright posture and two zygodactyl feet (Iñigo-Elias 2007). Lories and lorikeets make up the **Loriini**, a tribe of the subfamily Loriinae of the Psittaciformes. They are characterized by their adaptations to feed primarily on nectar, pollen and fruits, with a particularity in their tongue: it is quite long and mobile compared to other parrots, and has elongated papillae on its tip, used to collect nectar and pollen by extending outwards when the bird is feeding on liquid or soft foods (Cornejo 2005).

Trichoglossus moluccanus, commonly and appropriately named **rainbow lorikeets** for their extremely colourful plumage (Fig. 1.2), is a species of medium sized true parrots included in this taxon. They are native from North and East Australia, Papua New Guinea, New Caledonia, Solomon Islands, East-Timor, Vanuatu and Indonesia (Fig.1.3), traditionally roosting in the eucalypt forests and woodlands of the continent but found in a wide variety of habitats nesting in trees with thick trunks, both native and exotic (Chapman 2005, Jaggard et al. 2014).

They are a highly mobile species that can travel thousands of kilometers for food, have generalised feeding and breeding requirements, and can quickly adapt to exploit new feeding and breeding resources. They roost in large and very noisy communal groups that can reach thousands of individuals, breaking up into smaller foraging flocks at dawn, comprising between 10 and 50 birds (Higgins 1999).

Fig.1.2. Rainbow lorikeet (*Trichoglossus moluccanus*).

Individual F6 from the Fugle Zoo population of rainbow lorikeets in Tommerup, Denmark. Photo by Catarina Rosa, December 2018.

They are also quite often seen in mixed-species lorikeets flocks (Chapman 2005). These lorikeets are competitive feeders, aggressive to conspecifics or other birds, establishing relationships of dominance (Higgins 1999, Bruce 1973), although the population social dynamics are yet to be fully understood.

There is also evidence on the incredible flexibility of the vocal behaviour of the *Trichoglossus moluccanus*, with a study by Serpell from 1979 showing that the characteristics of their acoustic communication are passed on through cultural imitation of not only conspecifics but also calls from other species and non-vocal sounds picked up from the environment. Oddly, this topic has not been investigated further, with one exception being Baker in 2014 who studied the possibility of a founder effect in the vocalisations of bottlenecked populations of rainbow lorikeets in 3 call types defined by Serpell and found that there is no loss on the diversity of the repertoires, possibly a direct consequence of a fast evolution in the acoustic signals (Baker 2014).

The adjective “odd” is used because this species is, as a matter of fact, a successful and growing urban colonizer in Australia. Both because of their impressive generalist requirements and due to escapes from private owners, it is declared an agriculture pest since last century and an invading species throughout West and South Australia, all the way to New Zealand. There is a feral population in Perth and remarkable population growth in major Australian cities, such as Sidney, where they roost in gardens and parks. (Baker 2014, Lamont & Burbidge 1996, Jaggard 2014). They cause several nuisances to resident humans and other animal species, although they are drawn to the cities due do the abundance of flowers planted by gardeners and the seeds provided by delighted bird lovers (Lill 2009, Rollinson et al. 2003), which has boosted growth up to an estimated 35 000 birds (Daoud-Opit 2011) in urban flocks.

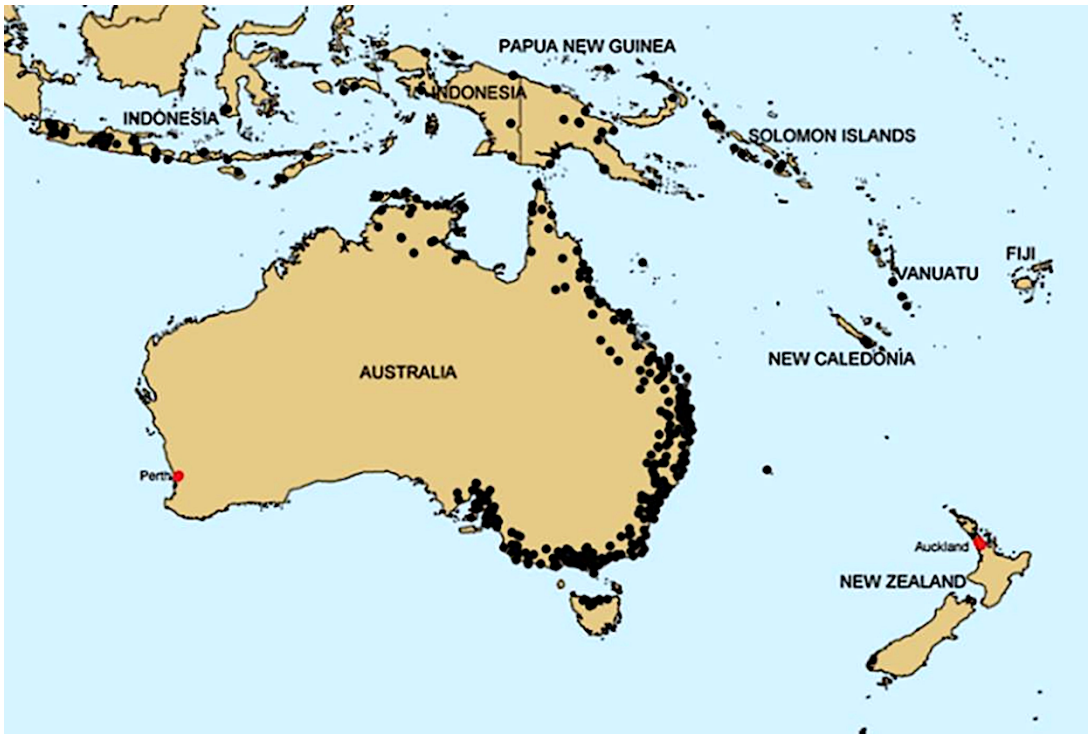

Fig.1.3. Map of the distribution of the rainbow lorikeet, *T. moluccanus*.
In black is shown the natural distribution, in red the introduced distribution. Image retrieved from the Department of Primary Industries and Regional Development of the Government of Western Australia. Available at https://www.agric.wa.gov.au/birds/rainbow-lorikeet [Retrieved on 20 October 2019. Page last updated on 30 May 2017]

1.6 Goals of research and predictions

Even though these numerous populations of rainbow lorikeets are living in such proximity to humans, there is very little research done on this species, and this trend is verified for all parrots; they might just be the most famous birds with the least amount of research done one them in the wild (Iñigo-Elias 2007). With this thesis I aim to start bridging that gap, by describing a healthy captive population and correlating the observed behaviours and vocalisations with hypotheses on vocal learning and evolution of cognition. Furthermore, I discuss how parrot individuals living under human care and invasive wild populations can contribute to the understanding of their species and basic scientific themes.

Just as other parrots, rainbow lorikeets are highly social and communicative birds, and exhibit a high range of vocalisations during their interactions. However, their detailed vocal and behavioural repertoires are yet to be properly studied, let alone properly documented (references for vocalisations are only found in Higgins 1999 and Serpell 1981). It is still to be discovered if this species has indeed a good learning ability, if it shows functionality in its calls, and even how the group behaves socially or how mating occurs.

With this in mind, it seemed only fitting that the study of rainbow lorikeets starts with the species' ethogram (Gerhardt 1992), for a detailed account of the behaviours observed. After this first goal, the dynamics of the population were described and analysed on the group and mating pair levels. The third goal was the description of the vocal behaviour, through the discrimination and characterization of call types, the correlation between behaviours and call types, and the characterization of the acoustical variation. This was done through recordings of the usual, mostly undisturbed routines of the flock.

My predictions included the reflection of group dynamics through the behaviours of the individuals, including the management of the hierarchy, as well as finding the mating pair at the core of the social network. On the matter of the vocalisations' analyses, I expected to find the correlation, mentioned above, between behaviours and call types to be significant, similarities in the vocal behaviour and acoustic characteristics between females and males, and interindividual variation in said acoustic characteristics.

Starting with a small-scale, zoo population study can prove to be a stepping stone to further research on the species and, along the line, on big scientific questions whose answer still remains to be dug up.

Fig. 1.4. Painting from 1772 of a rainbow lorikeet (*Trichoglossus moluccanus*) by Moses Griffith (1747-1819), the suggested earliest painting of an Australian bird.

– 2 –

METHODOLOGY

2.1 Experimental subjects

This project took place in the island of Fyn, in Denmark, in collaboration with the Sound Communication and Behaviour research group in the Odense campus of the Syddansk Universitet (SDU) – University of Southern Denmark – as well as the Danmarks Fugle Zoo. The latter is a zoological park located close to Odense and the SDU campus, in Tommerup, housing 800 birds of different species from all around the world in several aviaries over 6 hectares.

Between July to October 2018, birds of three species in the Fugle Zoo – rainbow lorikeets, mitred parakeets and orange-winged amazons (*Trichoglossus moluccanus*, *Psittacara (Aratinga) mitratus* and *Amazona amazonica*, respectively) – were fed on two new platforms installed in their enclosure. The process aimed to show the birds that the foreign object posed no threat and is actually associated with something good, such as suggested by evaluative conditioning. This concept is defined as an "attitude formation or change toward an object due to that object's mere co-occurrence with another valenced object or objects" (Jones et al. 2010), or, in common zoo keeper and behavioural biologist nomenclature, habituation. In this process, the birds might change their attitude towards the platform by having it associated with a reward: their food. Through this, it was possible to choose the focal species for the project, in this case the only species to show an improved positive response, as a group, to the platform and to being in close human contact: the ***Trichoglossus moluccanus***. This group of rainbow lorikeets proved to actually be quite neophiliac, which was unexpected since most parrots are found, from experience, to be very neophobic (Fox & Millam 2007) and started eating and comfortably standing on the platform since the first day.

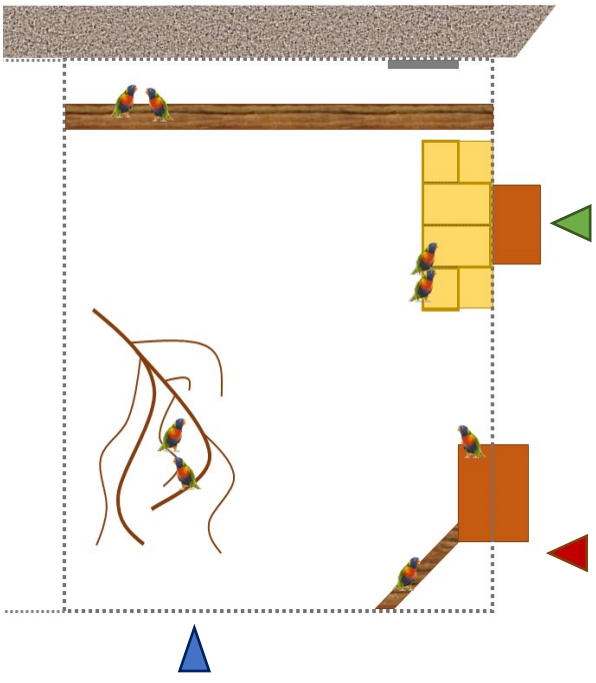

Fig. 2.1. Schematic of the rainbow lorikeet enclosure at the Danmarks Fugle Zoo.
Measurements: 3x2x2 meters (length, width, height). Recording spots indicated by triangles. Blue triangle: net + branches; red triangle: feeding platform + pole; green triangle: setup platform.

The recorded group was composed of 11 rainbow lorikeets. According to the park owner, Hans Åge Hjeresen, "two or three" individuals had come from a private owner in Denmark, that donated them to the Fugle Zoo, and all other had come from Knuthenborg Safaripark in Denmark. The previously privately-owned specimens were approximately eight years-old, and the ones originally from the safari park between eight and ten years-old. They had all lived in the Fugle Zoo for approximately six years.

These birds were housed in a 3x2x2 meters space, with an outdoor area and an indoor area, in the last enclosure of a row of 3 (Fig. 2.1). This meant that one of the net walls of the outside area was shared with the middle enclosure, in which a single olive-headed lorikeet (*Trichoglossus euteles*) lived, while the other two net walls were open to the park's visitor space. On the first and leftmost enclosure of the row, two chattering lories (*Lorius garrula*) were housed. The back and fourth wall of all the enclosures was cement,

with wooden nests attached, and one doorway to the indoor feeding area, on the right end. As seen on Fig. 2.1, the rainbow lorikeets share a big wooden pole close to the back wall, a smaller wooden pole on the right-hand corner, and branches on which to perch. The ceiling was almost all made of net, with about 1 meter of roof close to the back wall, and the floor was natural flooring, with dirt, stones and, occasionally, snow.

In their daily communal dish of food, provided by the Fugle Zoo staff every morning in the indoor feeding area, they got fruit, some of it mashed and some of it whole, as well as seeds and some parrot feed. The fruit, donated by local supermarkets, was very varied, generally seasonal, and sometimes locally produced.

2.2 Data collection

Setting up and data collection stretched from October 2018 to February 2019. These months allowed for an increased habituation of the birds to my presence. This proved essential to habituate the birds to the presence of a more constant observer. They were fed on the platform, before their daily feeding by the park staff, so they would regard my presence as a positive event, and the birds quickly started expecting me at the platform upon arrival for a recording session, indication of a successful association. Several fruits were tested in order to check for any that was not appreciated, and also to renovate the birds' interest, since they showed such neophilia; it was found that this group in general appreciates peach, grape, pear, banana, and that only some individuals were interested in plum and blueberries.

2.2.1 Individual recognition

A strategy for distinguishing the individuals had to be drawn. 75 percent of parrot species have no sexual dimorphism (Bercovitz 1987, Bendheim 1999), which means there is no clear distinction to the human eye between males and females, and that includes the rainbow lorikeets (Owen 2016). However, quite soon it was clear that males and females behave quite differently. The mating ritual is in itself a clue as to who is which, being that the male courts the female and later mounts her. As soon as any part of a mating ritual occurred between two individuals, I recorded who should be male or female, and described the birds according to morphological characteristics and/or their identification rings.

Since rainbow lorikeets form lifelong bonds (Higgins 1999), identifying a couple as a mating pair would come from frequency of cooccurrence; indeed, the assigned partners spent most of their time together. Each individual was codenamed as female (F) or male (M) and by mating pairs 1 to 4, followed by two females that have no mate. These were identified as females from other males' courtship events.

The following list describes characteristics for identification of each individual rainbow lorikeet in the Fugle Zoo group:

- **F1** – suffers from stress feather-picking; easily identified by having a completely naked breast and upper back, and a long, deformed beak. Silver ring, left foot.
- **M1** – permanently dirty tail feathers.
- **F2** – electric-blue breast feathers. Silver ring 027 LDF, left foot.
- **M2** – orange ring F75, right foot.
- **F3** – worn-out red ring (pinkish), left foot.
- **M3** – broad silver ring, polished, with 18 on it, left foot.
- **F4** – silver ring 18, with red worn-out stripe.

- **M4** – first to alarm, frequently perched on the setup. Purple ring LDF 15 R 350, right foot.
- **F5** – electric-blue breast feathers, permanently humid. Green ring, right foot.
- **F6** – exhibits limping and right paw bulbous deformity. Very social with me.
- **U1** - silver ring F75

Note that correct assignment of sex is impossible without genetic testing, or of course the observation of egg laying (our childhood teachings will tell us who is the female then), hence the discrimination of the sex in this population could prove to not be real. Even an encounter with sexual behaviours could prove misleading, since same-sex sexual encounters are found in many species of animals with diverse functions: establishment and reinforcement of hierarchy, as a social glue to form alliances and prevent conflict, or even because of mistaken identification of sex or maladaptation (due to life in captivity) (Bailey & Zuk 2009). Nevertheless, all behavioural observations indicate that these could be correct assignments.

2.2.2 Recording sessions

Every day upon arrival for data collection, from December 2018 to February 2019, the rainbow lorikeets came to the platform, vocalising loudly towards me, the newcomer, and expecting food. However, as soon as there was food on the platform for the first time of the day, they increasingly ignored the observer's presence more and more. They might restart vocalising towards the food container if the food ended, and, if the food bits were replenished, they would quickly go back to ignoring human presence. This is an important clue for the authenticity of the behaviours and vocalisations recorded during the session. It was, nevertheless, important to avoid any sudden and/or abrupt movements or sounds during the recording session, as that caused alertness in the group. Still, some individuals were more comfortable with human presence than others.

The recording sessions proceeded as follows:

1) Arrival at the Fugle Zoo in the morning, with the arrival time varying between 9h30 and 10h30, and picking of one available fruit from the park feeding kitchen, chopping it to small pieces.
2) Arrival to the enclosure and assembling of the recording setup.
3) Start of recording, with videos between 1 and 20 minutes long. Recordings were done on three spots: platform+pole, setup, net+branches.
4) Sometime during the session, the park birds (except the experimental subjects) were fed by the park caretaker. The subjects would be fed after the session, so they would not disappear into the indoor feeding area.
5) End of the recording session coinciding with the end of the battery for either the video camera or the recorder, sometime between 12h00 and 14h00.

Notes were taken during each video of who were the individuals in shot, which was their comparative position to each other (for easier identification on the videos later on, especially since the birds are quite dynamic and move around a great deal) and, when possible, who was vocalising at which second of the video recording.

2.2.3 Recording setup

Sound and image were recorded by separate equipment, as shown in Fig. 2.2.

Fig. 2.2. Recording setup.
From up to down: Seinheiser shotgun directional microphone, covered by a Rycote Softie Slip-on windshield, Panasonic high definition video camera, and Olympus LS-100 recorder. Microphone and video camera were set on two different tripods, and cable-connected as such: microphone – recorder – camera.

Only the left channel was captured during sound recording, and the following equipment and setup was used:

- Sennheiser shotgun directional microphone.
- Slip-on windshield – Rycote Softie.

The microphone was mounted on a high tripod directly in front of the subjects for optimal capture of the vocalisations. The microphone was connected to an:

- Olympus LS-100 recorder, a multi-track linear PCM model.

The recordings were done in one channel with a sampling frequency of 48kHz.

For video capture, a Panasonic high definition video camera was used, model HC-V720, placed underneath the microphone.

The camera was connected to the recorder so that the input from the microphone was recorded into the video file. After establishing the settings for sound capture, with just enough gain to prevent clipping at the constant recording distance of 1 meter between microphone and subjects, and 48kHz sampling frequency, the settings for the sound recorder and video camera were kept constant during the recording period.

2.3 Analysis of the recordings

A total of 7 hours, 22 minutes and 25 seconds of good quality recordings and notes were obtained, during January and February of 2019. Since the output of the microphone and recorder became the sound input for the video camera, sound and video were perfectly synchronized, making it possible to analyse both at the same time and see, in real time, the coordination between behaviour and vocalisations.

The videos were analysed by playing them on VLC 3.0.7.1 media player, an open and free software, with a localized zoom tool for closer observation of the subjects; this proved very useful to detect minor changes happening during calling: in breath, in tension of the body, in small movements such as a slight raise of the tail or a contraction of the back muscles. Close-up observation made it possible to determine who was vocalising at a specific time, as well as describing the behaviours in detail. The localized zoom also allowed for better focus on an individual or a set of individuals at a time, particularly important when there were many individuals on the shot. It was important as well to crosscheck the identity of the subjects with the field notes for every video.

For each vocalisation in the video, the audio clips of each were cut from the audio file of each video using Audacity 2.1.0, an open and free software as well. This sound editing program allows for the visualization of audio with a simple spectrogram and for the clipping of select segments of the audio file, saving them as separate files. The grey-scale spectrogram view was used, which made the vocalisations very clear against the noise background of the recordings. Complex bird songs can typically consist of partitioned syllables or notes, identified by a continuous sound between two silent intervals or by a sudden change in frequency (Tchernichovski 2000), but calls are generally shorter and simpler vocalisations, easier to isolate. Only clips that had clearly discrete calls were kept, i.e. with no overlap with other vocalising birds (either rainbow lorikeets or loud surrounding birds in the park) or other loud noises overshadowing it visibly in the Audacity spectrogram (such as park visitors or machinery).

2.3.1 Video analysis

For every video analysed, individualized vocalisations and behavioural patterns became part of a Microsoft Excel database spreadsheet, entered in chronological order for each video. The vocalisations were isolated if they were a call composed of either a continuous sound or of pulses, emitted by a single lorikeet inside a 1-meter radius of the recording setup. If the same individual emitted several sounds sequentially, these were clipped with a minimum interval of 0.1 seconds. Each entry had the several contextual parameters noted down, including a subjective naming of the calls, and with later analysis it became the call types.

Every vocalisation was associated to the behaviour performed by the birds. The individualized behaviours with no associated vocalisation were noted down as well on the same spreadsheet, with *sender behaviour* and *receiver behaviour*, so as to note down the response to each behaviour. This method stems from the rule that a behaviour is only validly classified as such if there is a consequence, that can, however, come for the bird itself (Martin and Bateson 2007). If this later was the case, the *receiver identity* and *receiver behaviour* would be classified as NA.

A total of 1846 relevant entries formed the data base (a length verified from similar studies in literature to be a good amount of data for analysis), of which 1480 were call entries and respective details and the remaining non-vocalising behaviours. The whole database was used for behavioural and demographic statistics. These entries came from 16 different videos, filmed on 6 separate days in January and February 2019.

2.3.2 Behaviour analysis

Based on database and having acquired a substantial knowledge of this rainbow lorikeet population's repertoire, I built an ethogram out of the observations. This is a valuable tool in descriptive research and in behavioural science, as it sums up the behaviour patterns of a population and/or species, catalogued with descriptions of each. The context of each behaviour is the structure of the ethogram, in the form of categories, since it is argued that removing the behaviour from its context is to merely take one element out of a hugely complex chain on the life of the individual (Gordon 1985). Since the distinction and description of behaviours is highly subjective, three people working in areas different from Biology and from each other were consulted on the accuracy of the distinction between each entry on the ethogram. As a consequence of this, three previously separate behaviours became nested under the "head jerk" behaviour. Additionally, a behaviour research group from the Faculty of Science of the University of Lisbon – EcoComp – was consulted as well and agreed to the final list.

2.3.3 Calls analysis

Upon finishing the database, there was a large number of call designations. Since it was meant to be just as a starting point, many of these designations were redundant. Therefore, I went through the audio clips again, one by one, and sorted them into folders of call types. Since there is no previously published vocal repertoire of rainbow lorikeets (Higgins 1999 and Serpell 1981 mention the vocalisations of *T. moluccanus* in passing and their context, but do not go deep into their acoustic analysis), the names are subjective suggestions, or coming from similarity to calls described in other species. To qualify for call type, the folder needed to contain more than five good quality audio clips (calls) and made by more than one individual (Montes-Medina et al. 2016). If these prerequisites were not fulfilled, the calls would go into the *other* folder.

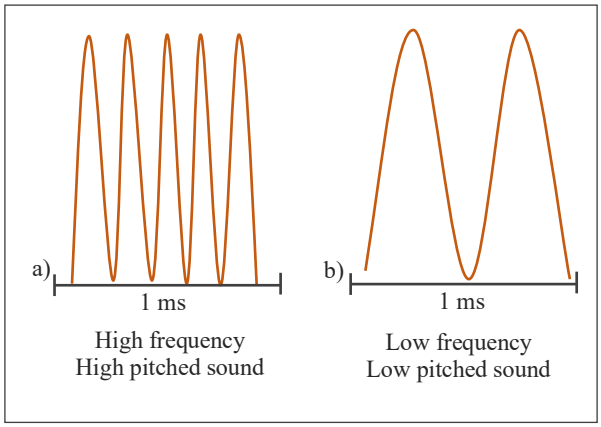

Fig. 2.3. Association between frequency and pitch. Diagram of a) a signal with high frequency, b) a signal with low frequency, with the same duration of 1 millisecond. High frequency soundwaves are interpreted as high pitched sounds, while low frequency are interpreted as low pitched sounds.

Quantifying call and song similarity between situations, individuals, or even populations and species is notably difficult and easily subjective (Tchernichovski et al. 2000). So far there is not a standard method, but there are some commonly used techniques. The acoustical analysis of the call audio clips was done using R 3.6.0 through R Studio 1.2.1335 for MacOS X 10_14_6. Each selected call type was analyzed separately, starting with exploratory oscillograms, frequency spectra and spectrograms, obtained with the functions plot() from the *graphics* package and spec() and spectro() from the *seewave* package. The spectrogram is a widespread visual representation of sound (Tchernichovski 2000), displaying the amplitude of the frequency components of the signal over time – time is the horizontal axis, frequency is the vertical axis, and amplitude is the shading of the frequency content (becoming a three-dimensional plot) (Thorpe 1954). Due to practical issues regarding microphone calibration, the only measure of sounds pressure used is relative amplitude, and there is no comparison of amplitude between calls in this analysis.

This preliminary visual run-through allowed for the discard of clips with too much noise and the selection of the ones with the "cleanest" sounds. All clips were subject to a Butterworth bandpass filter with a lower cutoff frequency of 500Hz and a higher of 16 kHz before any analysis. Furthermore, since sex and sender were expected to have an influence in the vocalisations, calls coming from U1 or from an unidentified caller (NA) were removed from the statistical analysis, resulting in 893 calls from identified senders.

The resulting database, composed of these 893 good quality call files, was subjected to the analysis of several acoustical parameters, chosen from literature on well-described call analysis of Psittacidae, from species such as budgerigars (*Melopsittacus undulatus*), Llilac-crowned amazons (*Amazona finschi*), Peach-fronted conures (*Aratinga aurea*) and orange-fronted conures (*Aratinga canicularis*), and another bird species as an outgroup, great cormorants (*Phalacrocorax carbo sinensis*) (Brittan-Powel et al. 1997, Montes-Medina et al. 2016, Thomsen et al. 2013, Adams et al. 2008, Mäkelin 2018, resp.). Parameters

related to amplitude, colloquially translated into the volume or loudness of a sound, were not as used in literature as frequency parameters, and moreover there was an issue with the microphone calibration for amplitude, and so they were left out of the analysis.

The following parameters from these references, that were noted down for every clip of the data base, are listed below, as well as the functions [displayed as function()] used to obtain them and the R *origin package*:

- The duration of the call – duration(), *seewave* package (Sueur et at. 2008).
- The number of pulses in the call – timer(), *seewave* package, with a Hilbert amplitude envelope with 20% threshold of relative amplitude, 0.006 seconds of minimum duration, and mean sliding window of 50 points of window length and 0 overlap (Fig. 2.4).
- The number of frequency peaks – the peaks from the mean frequency spectrum (obtained with meanspec() with a window length of 512 and 90% overlap) are calculated through fpeaks() (created by Jerome Sueur and Amandine Gasc), *seewave* package, with a 25% threshold of relative amplitude, a relative frequency threshold of 400Hz, and amplitude slope of 0.1 on both peak sides (Sueur 2018) (Fig. 2.5).

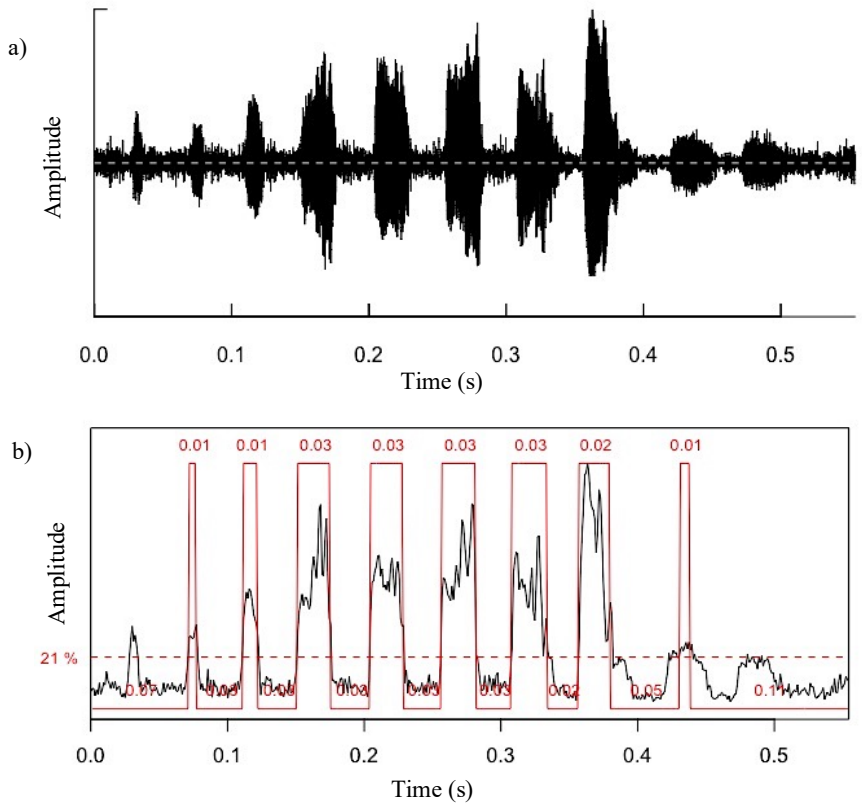

Fig. 2.4. Outputs of analysis of the number of pulses on R Studio on a recorded *trill* call, with functions from *seewave* package.
a) oscillogram of the Butterworth bandpass filtered wave, obtained through the oscillo() function. b) output of the timer() function, which contains and plots the duration of signal periods and pause periods, calculated from a Hilbert amplitude envelope with 20% threshold of relative amplitude, 0.006 seconds of minimum duration, and mean sliding window of 50 points of window length and 0 overlap. In red over the plotted wave are the detected pulses and their duration in seconds.

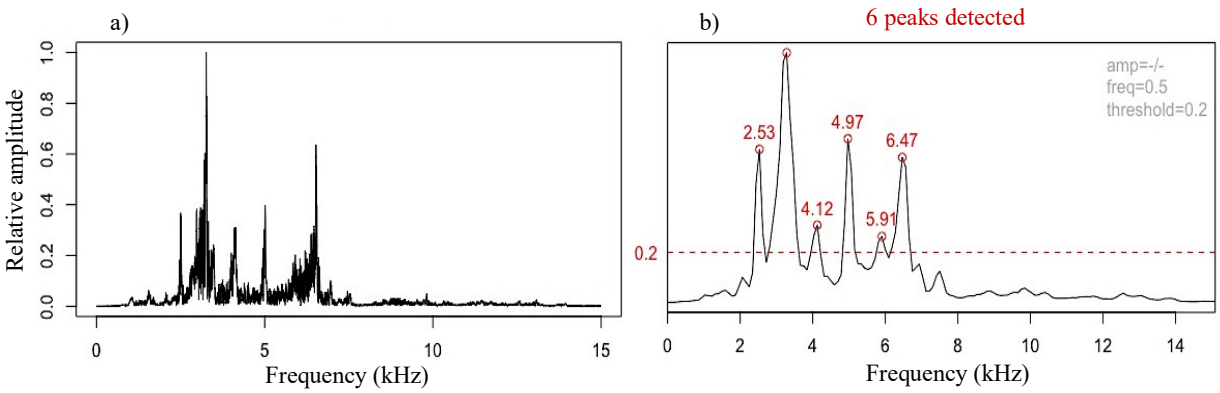

Fig.2.5. Outputs of analysis of frequency peaks on R Studio on a recorded *very high pitched* call, with functions from *seewave* package.
a) frequency spectrum of the Butterworth bandpass filtered wave obtained through spec(). b) mean frequency spectrum, through meanspec(), with a window length of 512 and 90% overlap, showing detected frequency peaks by means of fpeaks() with 25% threshold of relative amplitude and a relative frequency threshold of 400Hz. In red are the frequencies of the detected peaks.

- The peak frequency (kHz) – the frequency peak from fpeaks() with the highest relative amplitude, making it the frequency value of highest energy in the call.
- The frequency bandwidth – the difference between the highest and lowest frequency.
- The average repetition rate – no. of pulses per unit of duration (pulses/second).
- from specprop(), authored by Jerome Sueur and Caroline Simonis, with a patch by Jesse Ross (Dec. 2012), from the *seewave* package:
    - frequency mean - the centre of the distribution of power across frequencies
    - median frequency
    - frequency standard deviation
    - SEM – standard error of frequency mean
    - Q25 – the first quartile of frequency values
    - Q75 – the third quartile of frequency values
    - IQR – the interquartile range of frequency values, that is, Q75-Q25

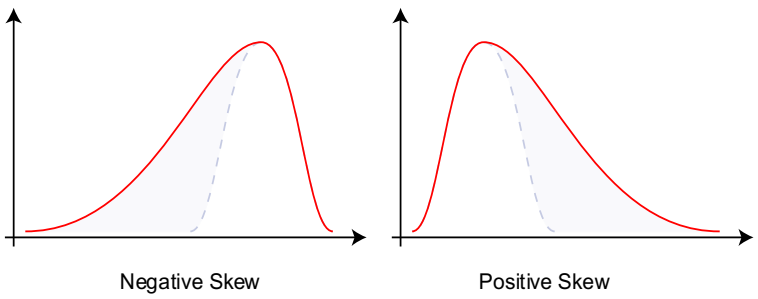

Fig.2.6. Diagram of signal skewness in a plot.
Image from Wikipedia, The Free Encyclopedia, available at https://en.wikipedia.org/wiki/Skewness#/media/File:Negative_and_positive_skew_diagrams_(English).svg. [accessed on October 18 2019]

- frequency centroid – the location of the centre of mass of the frequency spectrum, that is, the weighted mean of the frequencies present in the call
- Kurtosis – measure of peakness (characterizes whether the frequency spectrum has more items in the centre, shoulders or tails)
- Precision – resolution of the spectrum
- Skewness – measure of asymmetry of the frequency spectrum. $S < 0$ when the spectrum is skewed to left with the tail on that side, $S = 0$ when the spectrum is symmetric, $S > 0$ when the spectrum is skewed to right with the tail on that side, and spectrum asymmetry increases with $|S|$ (Fig. 2.6)
- Evenness – Shannon spectral entropy, a measure of the disorder or uncertainty of the information in a signal, indicating the predictability of the signal. The entropy of a noisy signal will tend towards 1, whereas in a pure tone signal it will tend towards 0 (Wan et al. 2018). It is calculated through the ratio between the sum of average relative amplitude of the frequencies in the signal and the number of frequencies (Fig. 2.7)
- Flatness – the measure of spectral flatness, also called Wiener entropy, calculated as the ratio between the geometric mean and the arithmetic mean. A noisy signal will have a flatness value tending towards 1 whereas in a pure tone signal it will tend towards 0 (Jerome Sueur in R Studio)

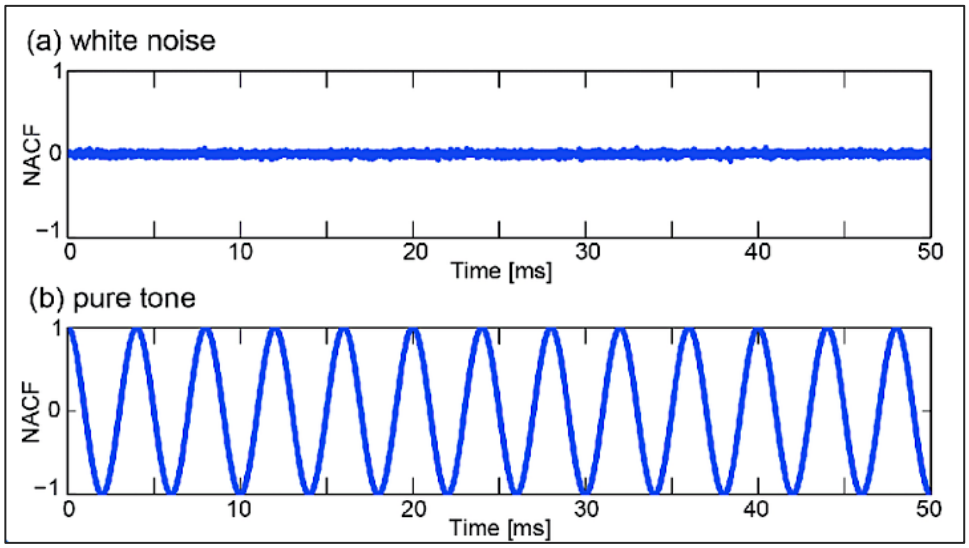

Fig.2.7. Examples of white noise and a pure tone.
a) would have an evenness with value close to 0, while b) will have evenness close to 1. Adapted image retrieved from Psychophysiological Evidence of an Autocorrelation Mechanism in the Human Auditory System - Scientific Figure on ResearchGate. Available from: https://www.researchgate.net/figure/Examples-of-the-NACF-for-a-white-noise-b-pure-tones-c-the-human-voice-and-d_fig2_315855026. [retrieved on 18 October 2019]

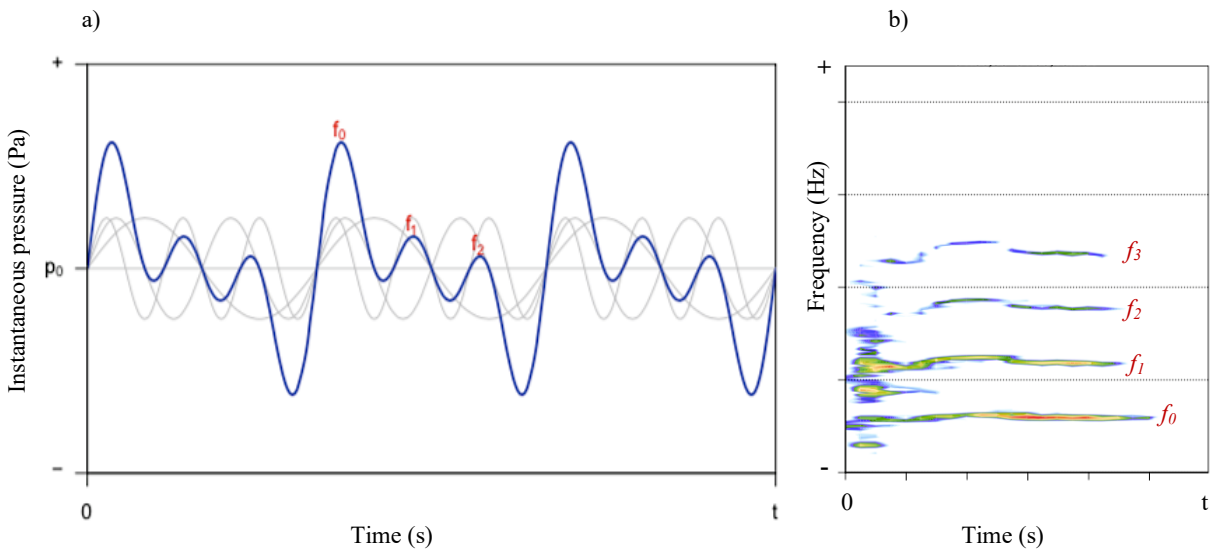

Fig. 2.8. Harmonics in sound waves.
a) Diagram explaining the occurrence of harmonics. Image retrieved from Sueur, J. (2018) with the following legend: "Harmonics. Sound made of three tones with a harmonic ratio: the fundamental (f_0), the first harmonic (f_1) and the second harmonic (f_2). The light gray lines correspond to these three tones isolated.". b) Spectrogram of a *very high pitched* call showing a clear harmonics series. The lowest line represents the fundamental, f_0 the sine wave with the lowest frequency, and the three lines above are harmonics 1, 2 and 3, whose frequency values are perfect multiple integers of the fundamental.

Furthermore, the existence or absence of harmonics were explored as descriptive characteristics, also through fpeaks(). Most sounds in nature are compositions of sine waves of several frequencies, making them acoustic complex signals. A sound wave with a harmonic series has its frequencies as multiples, with a lower frequency sine wave – called fundamental – and sine waves with higher frequencies that are perfect integer multiple of the fundamental (Fig. 2.8). In music, when a wave has harmonics, its sound in said to be harmonic sound. Music from a piano, for example, is harmonic, while music from cymbals is not. (Kostka et al. 2017).

2.4 Statistical testing

Statistical analysis was done using R 3.6.0 with R Studio 1.2.1335. The first exploratory tests were Mann-Whitney tests of medians, which examines if the medians of two samples are similar without needing an equal sample size. This is a non-parametric test, since the data did not verify the necessary assumptions, such as normality.

The next approach was submitting contingency tables (a table of frequencies) to a Pearson's chi-squared test with computation of p-values by Monte Carlo simulation, using chisq.test() from *stats* package. The test statistic and its p-value indicate whether there is a significant association between the two categorical variables in the table: the null hypothesis is that the variables are independent and the distribution of one is not affected by the presence of the other. The contribution of each cell value to the significance was discovered with an analysis of the standardized residuals, obtained by subtracting the expected value to the observed value for each cell while controlling for the contribution of the sample size of each cell. One of the analyses done was between call types and behaviour: whether the frequency of call types is independent of the frequency of all the behaviours. The call types that were recorded

more than expected in each behaviour, equivalent to a p-value significant when lower than 0.05, were considered the ones with standardized residuals higher than an absolute value of Z=-3.89, obtained from the standard normal table through the value 7.751938e-05, from a 645-cell contingency table (0.05/656=7.751938e-05) (Naioti & Mudrak 2018). The same test was performed for the frequencies of call types with behaviour categories, sender, and sex. For the associations to a behaviour category to be relevant, the value of the standard residual must be higher than Z=3.37 (contingency table with 135 cells and significance threshold of 0.05).

In order to discover which acoustical parameters best account for the variability in the acoustic characteristics of the calls, I performed a principal components analysis (PCA) on the data, using prcomp() from *stats* package. If the resulting principal components have an eigenvalue higher than 1, there is indication that the PCs account for more variance than accounted by one of the original variables in the data (Budaev 2010). The non-colinear variables in the chosen PCs with a variance contribution higher than 5 percent where the ones considered to have an important contribution to their principal component. This threshold is the expected average contribution, given by 1/(nº of variables) = 1/20 = 5.

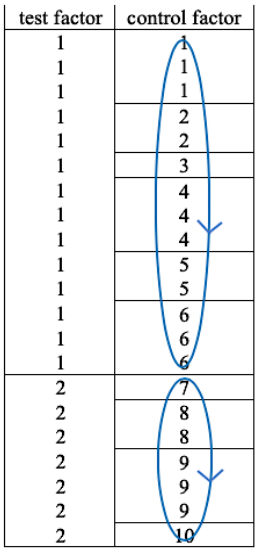

Fig. 2.9. Schematics of a permuted Discriminant Function Analysis (pDFA) with a nested design. Used for testing the discrimination of sex of the caller from the acousic parameters tested, with *sex* as the test factor (left column, 1 and 2) and *sender* as the *control factor* (right column, 1 to 10). The permutation is represented by the blue arrow, and happens only between individuals of the same sex. Figure adapted from a document provided by R. Mundry (Mundry & Sommer 2007).

These parameters, for each of the selected calls, were subjected to a permuted Discriminant Function Analysis (pDFA) to test the assignment of the call files to their call types, according to the variables – acoustic parameters – considered. The permutation approach allows the test to work with non-independence of the calls, since they are grouped together by a control factor, and these groups are then not disassembled during the test, i.e., the permutations acts in blocks. In this analysis' case, the calls belong to different individuals – the control factor – and the test factor would be the call types (Fig. 2.9). The pDFA was conducted using the functions written in R by Roger Mundry, in a script for R version 3.0.1, as used in Mundry & Sommer (2007), based on the function lda() of the R package *MASS* (Venables & Ripley 2011). An incomplete design was used since there were different numbers of calls by each sender and in each call type, using all available combinations of the levels of the test factor – call types – and the control factor – sender – to derive the discriminant function, so as to include all levels of the test factor (all 12 call types) in the analysis. It was done with 100 random selections of sender calls and with 1000 permutations. A p-value bellow 0.05 indicates that the calls are correctly assigned to the test factor through discrimination of the selected variables. The same analysis but with a nested design was used to test for the existence of differences in sex through acoustic characteristics, with sex as the test factor and sender as the control factor, since sender is nested in sex, and no restriction factor.

For each acoustical parameter obtained from the PCA, Generalized Linear Mixed Models (GLMM) fit by maximum likelihood and random slope and random intercept models were applied, using firstly behaviour category (9, since the 45 behaviours were too heavy for R to compute) and secondly call types

(12 of them) as fixed effects, and sender (the vocalising individual) as the random effect across contexts. This statistical tool tests how the fixed effects impact the explanatory variable – each acoustic parameter– while allowing for the influence of stochastic, or random, effects to be taken into consideration, while also solving the issue of non-independence, since the data has calls from the same individuals. The random intercept model accounts for different baseline differences in the acoustical parameter being tested between the different fixed effects, while the random slope model allows for the effects to have different slopes (Winter 2013). Although some of the parameters did not follow a normal distribution, the GLMM tests are considered to be quite robust against this violation of the normality assumption (Gellman & Hill 2007). Duration, SEM, Q25 and skewness follow a gamma distribution, while peak frequency, mean, IQR, evenness, bandwidth and average repetition rate follow a normal distribution. The main functions used were anova() from the *stats* package, and lmer() from *lme4*.

To test for individual differences in the acoustic characteristics of the calls, and since none of the parameters followed a normal distribution when plotted against either factor, Kruskal-Wallis and one way analysis of means tests were performed on each parameter for the two most common call types: *high pitched* and *short*. These analyses, also non-parametric, compare several samples for differences due to the wanted factor relying on rank-ordering, as a non-parametric alternative to ANOVA. For sex, the Mann-Whitney test was used again, because there were only two samples being compared (female and male values).

– 3 –

RESULTS

3.1 Behaviour

3.1.1 Overview of the ethogram of the rainbow lorikeets of the Fugle Zoo

The behaviours observed and recorded in the data collection sessions were divided into 9 categories: affiliative behaviour, agonistic behaviour, feeding, locomotion, maintenance, sexual behaviour, stationary, vigilance, and other. All behavioural categories include vocalisations, and the behaviours totaled 45 individualized behavioural patterns. These discrete behaviours are described in detail in the Appendix.

1) Affiliative behaviour

This type of behaviour is credited with creating and maintaining the social bonds between the sender and receiver. Since the mating pair bond is the archetype of affiliative relationships, it is natural to observe these behaviours most frequently between the couple (Emery et al. 2007). Indeed, all senders directed these behaviours to their mate in my observations, and most were received with either affiliative or neutral (stationary) behaviours (on 82% of the occurrences). It is the category with the lowest diversity of call types (7 out of 15 total call types). Very frequent before and after mating, and it seems to agree with the hypothesis that it maintains and strengthens the bonds between the pair (Campbell & Lack 1985).

Allopreening	**Allo**
Food sharing	**FS**

2) Agonistic behaviours

Conflicts arise mainly from competition during feeding, and they are an indicator of the hierarchy (Martin & Bateson 2007), including in the Fugle Zoo population. More dominant rainbow lorikeets will protect their feeding ground from any other individuals coming to feed, and it will often be a joint effort between the mating couple that is feeding. Agonistic interactions also occur between the mating pair, during feeding, as a response of attempted food sharing or food stealing, and during the mating ritual, as rejection.

These behaviours are observed twice as frequently as affiliative ones (10.2% against 5.3%). While chasing away's observed responses were 81% fleeing, snapping elicited a fleeing or a snapping response, both with a 20% frequency. Standing tall only had fleeing as a response (25%)

Chasing away	**CA**	**Snapping**	**Sn**
Fleeing	**Fle**	**Standing tall**	**ST**
Patrolling	**Pat**		

3) Feeding

The rainbow lorikeets were recorded on the outside area of their enclosure, which meant all feeding during data collection happened with food provided by me, either on the feeding platform or the setup platform. Several pieces of fruit were provided simultaneously, and if the food was finished, I would replenish it sometime after. This way, the recording happened on a simulation of foraging conditions, since food was not unlimitedly available, and the hierarchy of individuals was revealed through the access to the feeding spot (further developed in the Hierarchy section).

This was the most commonly observed category of behaviours (34.9% of all behaviours counted, in which chewing – 15.8% – and feeding – 11.8% – were some of the most frequently observed) and had the most diverse call type occurrence, with every call type recorded with these behaviours. Chewing was the most recorded singular behaviour, with a 15.5% frequency. For stealing, 51% of the responses of the receiver are a continuation of feeding and chewing, with no attempt to try to prevent the taking.

Asking	**Ask**	**Searching**	**Sea**
Chewing	**Ch**	**Stealing**	**Ste**
Feeding	**Fee**		

4) Locomotion

Locomotion behaviours include any movement that takes the individual from one spot to another. This population displayed many ways of doing so, showing how agile and nimble rainbow lorikeets are, and they are commonly seen moving around the enclosure.

It was the third most common behaviour category observed (10.6% of behaviour count).

Climbing	**Cl**	**Side-stepping**	**SS**
Flying	**Fly**	**Take-off**	**TO**
Jumping	**Ju**	**Walking**	**Wa**
Landing	**La**		

5) Maintenance

The behaviours in this category include any action that will improve the condition of the body, the comfort and satisfy physiological needs of the bird.

It is the category with the lower frequency of calls associated (only 2.3% of all calls were registered occurring with maintenance behaviours), since these are solitary actions, with almost no associated interactions to other individuals, so most calls occurring were undirected (90% had no receiver). These actions happen for long stretches of time. Preening is the most common maintenance behaviour (51.6% of total behaviour count in this category).

Beak gapping	**BG**	**Preening**	**Pree**
Beak rubbing	**BR**	**Scratching**	**Scr**
Defecation	**De**	**Sneezing**	**Snz**
Fluffing	**Flu**	**Stretching**	**Str**
Foot biting	**FB**	**Tail wagging**	**TW**
Head shake	**HS**		

6) Sexual behaviours (listed in chronological order)

Sexual behaviour was observed during the whole period of data collection of this project, starting in December 2018. According to Higgins, the breeding season for rainbow lorikeets varies extremely between regions: in the whole of the Australian country, the species has been recorded breeding every month except March (Higgins 1999). This means it was no surprise that the behaviour was observed, and the Fugle Zoo population is noted by the owner Hans Hjeresen for breeding frequently.

Two events of mating were recorded during data collection, of which one was fully recorded, with the predating and postdating moments (Appendix 6.1). These events involved two paired couples, 2 and 3, and one extra-pair occurrence, between M3 and F5. This last one was composed of courtship by M3 and rejection by F5, and interrupted upon the arrival of F3, that lead to M3 joining her in feeding. The events between coupled partners resulted in mating. All mating pairs were observed performing courtship.

Below are the seven discrete behaviours that compose the full mating ritual, here displayed in order of occurrence, of which allopreening is not exclusive, since it occurs in affiliative situations. Attempted

mounting is named thus since 57% of its responses are null and 28% are snapping, leaving a small margin of success.

Allopreening	**Allo**
Courtship	
• Bobbing	**Bob**
• Hissing	**Hiss**
• Attempted mounting	**AM**
• Rejection	**Rej**
Mating	**Mat**
Post-coital	**PC**

7) Stationary behaviours

This category describes the times for stillness, which are a big part of the day for these birds.

As some of the most frequent singular recorded behaviours (12.5% for perching and 5.3% for hanging), 17.8% of the total count of behaviours were stationary. This category is also associated with a great diversity of call types, with all being accounted for during these behaviours.

Hanging	**Ha**
Perching	**Per**

8) Vigilance

This category includes behaviours observed on the imminence of any threat coming close to the enclosure. These were most commonly cats of the Fugle Zoo and could also be a response to vigilance calls of the birds in surrounding enclosures.

Alarm	**Ala**
Alert	**Ale**

9) Other behaviours

The behaviours in this category have no associated response, meaning that they lack a possible inference of function, or a similar behavioural description in literature. This can be due to lack of sampling or rarity of occurrence. Adding to the difficulty of understanding their function, responses are mainly neutral behaviours (stationary or feeding) or mirroring the behaviour itself.

∩-bob	**∩B**	**Neck stretching**	**NS**
Foot shoving	**FSo**	**Shiver**	**Shi**
Head jerk	**HJ**		

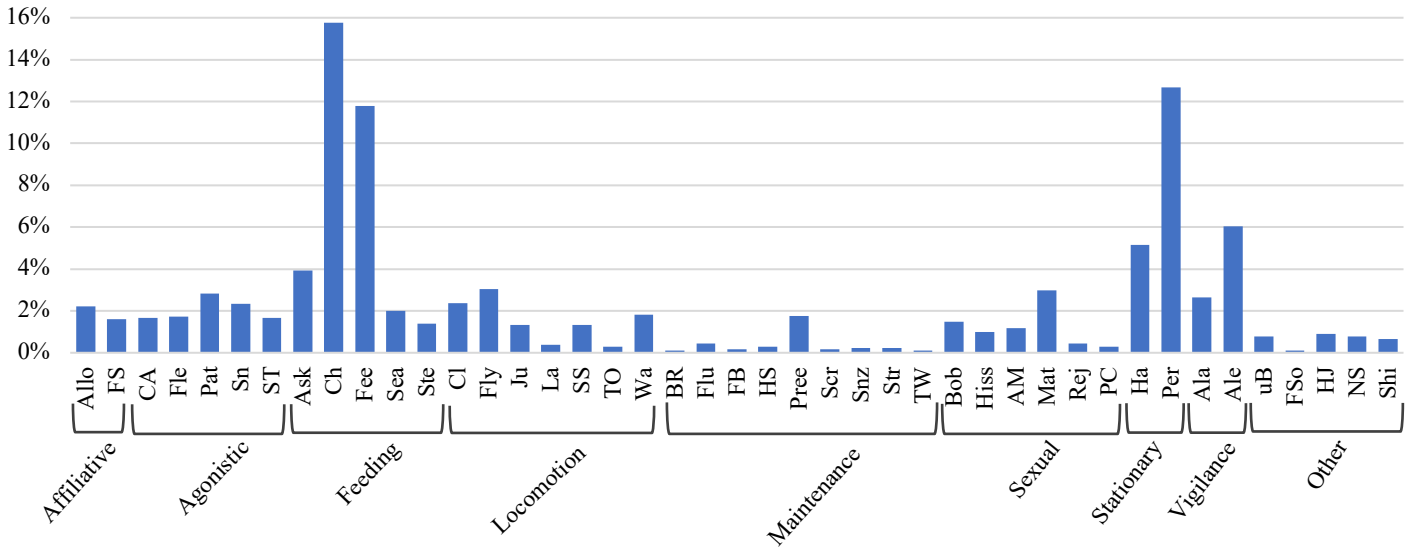

Fig. 3.1. Relative frequency of occurrence of recorded behaviours, ordered by behavioural category.

3.1.2 Population dynamics: Individuals, mating pairs and hierarchy

The most frequently recorded individuals were F3 and M3, the mating pair that dominated the feeding platform, causing a retreat of the other individuals upon their arrival. They are the ones that obtained the highest number of victorious outcomes and the smallest number of defeats out of agonistic encounters. Indeed, when F3 and/or M3 were feeding in the platform, no others would stand on it for long. They might stay close and timidly try to take a piece and feed on it somewhere else, whilst the mating pair would patrol the platform frequently and chase away the other individuals. They were the couple recorded mating from beginning to end, maybe since they dominated the space to do so undisturbed. They vocalised confidently towards me to ask for food if there was none or the available one was not of their liking.

F1 and M1 were a very reclusive mating pair, rarely appearing close to the net and keeping more to the back of the enclosure, close to the nests. Even when coming to the recording radius, they would keep to themselves and interact little with others. Since F1 had a naked breast, it could be due to her need of protection from cold and other adverse weather conditions. Even though M1 was identified by having permanently dirty tail feathers, he was not observed preening himself in the observation radius, or being allopreened by F1. They were not at ease with my proximity, retreating quickly whenever I approached to record or replenish the food stock.

F2 and M2 were almost always seen together, moving around a lot in the enclosure. They seemed to be midway in the hierarchy, not evading other individuals while also not getting into conflicts. F2 was very fearful of me coming close.

F4 and M4 dominated another spot in the enclosure, the setup platform. M4 was very active and loud defending this spot, while F4 fed peacefully with his protection. Furthermore, M4 was quite frequently

the first rainbow lorikeet to call out in alarm to imminent threats close to the enclosure, such as the park's resident cats.

F5 was skittish and shy, and received the most agonistic interactions, retreating or fleeing very fast. She was commonly close to the feeding platform and tried to get any pieces of food she could. On account of this behaviour, she seemed to be low in the hierarchy. She seemed to have a peaceful relationship with F6.

F6 showed the most humanized behaviour of all. She was extremely trusting with my presence and was to only one to search for me, climbing to face height, vocalising towards me, even bobbing her head as if in courtship behaviour to ask for food, which she readily and gently took from my hand. Even though she was the target of frequent agonistic interactions, she did not flee with haste. Instead, she stayed close and snatched pieces of food confidently from the feeding spot, that she took with her somewhere else, slowly due to her limp, and ate with her paw up, unlike any other rainbow lorikeet. She was often seen on the floor, which could be due to limping, but F5, F2 and M2 were also seen there picking at leftover pieces of food, which could indicate a correlation between being lower in the hierarchy and lesser access to higher spots in the enclosure.

U1 was recorded in only one occasion, hence the lack of knowledge on even its sex. This could be due to a very low position in the hierarchy or to an extreme neophilia towards me and the new platforms. In fact, both factors could be reason for his absence.

On Table 3.1 the defeat score is displayed for each individual as a quantitative approximation of a measure of hierarchy, inspired by Clutton-Brock et al. (1979) and David (1988).

Table 3.1. Defeat score from agonistic interactions for all individuals in the Fugle Zoo population.
The score is calculated as the proportion of defeats (D) to the total of agonistic interactions in which the individual was the receiver, as in SCORE=D/(V+N+D), in which V represents victories and T are ties. In the left table the females are displayed, and in the right the males.

	V	T	D	Score
F1	5	1	1	0,14
F2	1	1	1	0,33
F3	29	28	15	0,21
F4	1	-	-	0
F5	-	15	31	0,67
F6	-	2	4	0,67

	V	T	D	Score
M1	0	2	1	0,33
M2	-	-	1	1
M3	26	33	19	0,24
M4	1	-	-	0
U1	-	-	2	1

3.2 Vocal behaviour

3.2.1 Vocalisation rates

Table 3.2. Total number of calls produced per individual for all analysed recording sessions, and percentage of the total of calls recorded.

Individual	Total	%
F1	49	3.31
M1	43	2.91
F2	51	3.45
M2	80	5.41
F3	333	22.50
M3	577	38.99
F4	47	3.18
M4	120	8.11
F5	93	6.68
F6	91	5.68
U1	4	0.27
TOTAL	1488	100

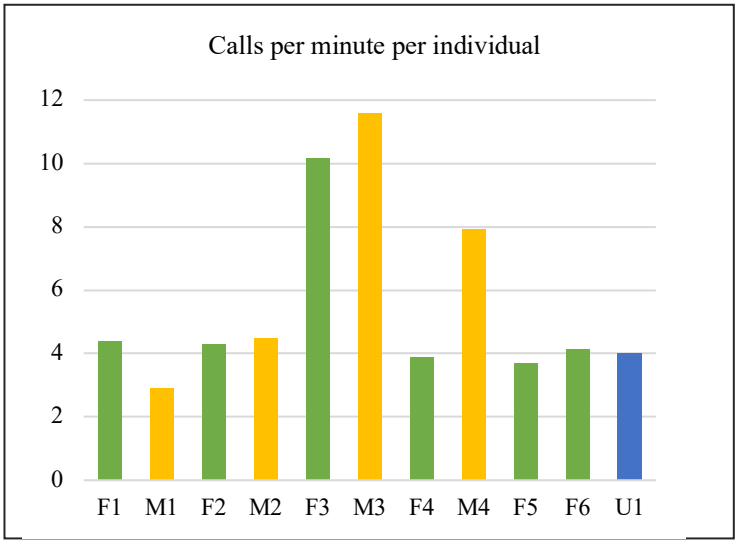

Fig. 3.2. Average number of calls per minute per individual.
Green represents the frequency of females, yellow of males, and blue of the unidentified sex of U1.

The rainbow lorikeet population at the Fugle Zoo vocalised extensively throughout the recording sessions (Table 3.2, Figure 3.2), when performing all kinds of behaviours, even though 60% of calls had no discernable receiver. For each individual, between 40% and 94% of their calls had no receiver. A small portion of calls, between 1 and 5%, were directed to me, asking for food. Almost all behaviours described in the ethogram included vocalisations of one or several types.

The individuals that were part of a mating pair vocalised mainly to each other: between 22% and 58% of their total of calls was directed to the mate. It was the main receiver of their directed calls. F5 and F6, females without mates, had different patterns: F5 vocalised to F3 and M3 (2 and 27%, resp.), while waiting to have access to food and being denied, and F6 had 94% of calls undirected, with a big portion (5%) directed to me.

By correcting for the differences in sampling size for each individual, the distribution of vocalisations per minute between the sexes is close to 50% each (Fig. 3.3). When applying a Mann-Whitney test, the difference between the vocalisation rates of the sexes is non-significant (Z=-0.540, p-value=0.589).

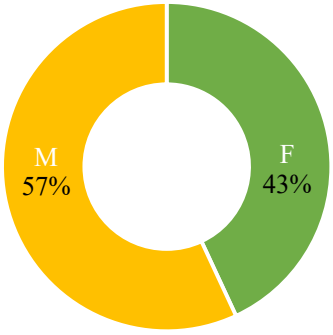

Fig. 3.3. Average frequency of calls between sexes (per minute of sampling).
Green represents the frequency of females, yellow of males. The difference is not considered significant (MW: Z=-0.540, p-value=0.589).

3.2.2 Call types

The initial list included 20 folders of call types: *annoyance, growl, gurgle, high pitched, hiss, mating, opera, parrot, peum, pi, pierce, pip, scream, screech, short, telephone, trill, whistle* and *very high pitched*. However, after selection of occurrence and number of senders, only 12 qualified for call types for analysis: *annoyance, growl, gurgle, high pitched, parrot, peum, pi, pip, screech, short, trill* and *very high pitched*. (Fig. 3.4)

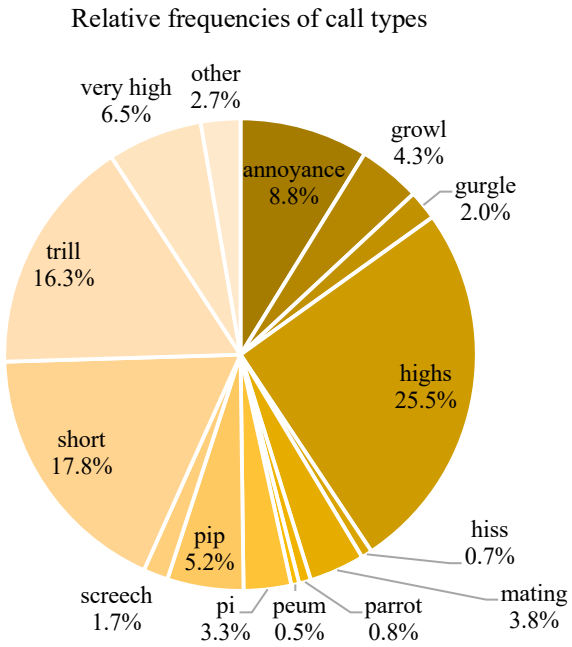

Fig. 3.4. Relative frequency of call types in the call data set.

The remaining became the *other* call type. *Opera* and *telephone* had only one audio clip each, *scream* had only two files from F5, and subject F6 made a particularly noteworthy contribution: *pierce and whistle* were calls made only by her, with between 5 and 10 audio clip each type. Even though *hiss* and *mating* were only recorded by M3 and became part of the *other* call type, they are included in the statistical analysis for their clear association with the mating ritual, which makes them relevant for the characterization of the sexual behaviour of this population. They were observed in M2 as well, although without a good audio recording. They were not, however, included in the acoustic analysis.

The call types and their acoustic characteristics are described in the Appendix (6.2).

3.2.3 Call type frequencies in the population

No individual was recorded performing all described call types, and different individuals used call types with different frequencies. This diversity was enough for a significant result from a Pearson's Chi-squared test ($X^2_{150} = 921.32$, p-value = 0.0004998), and is colourfully visible in Fig. 3.5.

U1 only has 4 calls recorded, of the *short* call type. Apart from this exception, the three most called out types, *high pitched*, *short* and *trill*, were recorded for all individuals, except F2 who had no evidence of *short* calls. Even though *growl* has low occurrence (only 4.3%), every individual was recorded using it. Similarly, *pi* was used by all except F1 and *very high pitched* by all except F6. *Hiss*, on the other hand, was only recorded on M3. I was also observed in M2, but outside of the recording radius.

The *pip* call type was very frequently heard coming from M4, from the top of the setup platform where he established his territory. However, many times he would go out of recording range while vocalising these calls, which excluded them from the analysis.

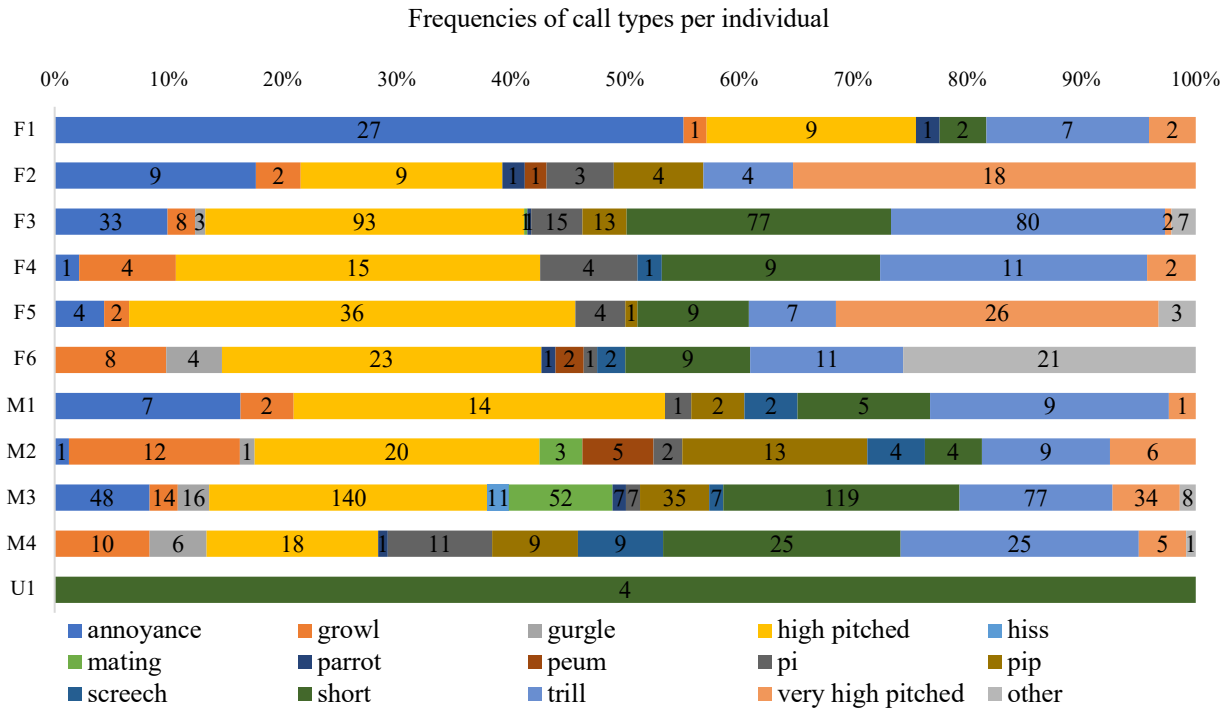

Fig. 3.5. Relative frequencies of call types for each individual, shown in percentage of total calls per individual. The number of total recorded calls per call type for each sender are displayed on the bars.

Noteworthy to say that F6 dominates the *other* call types, contributing with half of the calls on this category (21 out of a total of 40).

In terms of call types frequencies between the sexes, with correction for sample size of each individual, there is evidence of independency ($X^2_{15} = 6.0053$, p-value = 0.9797), indicating that females and males vocalise similarly not only in total numbers, as seen before, but within call types as well (Fig. 3.6). In fact, almost no call types were recorded in only one of the sexes. The exception is the *hiss* call, which is recorded only in M3, and is included in the other *call type*.

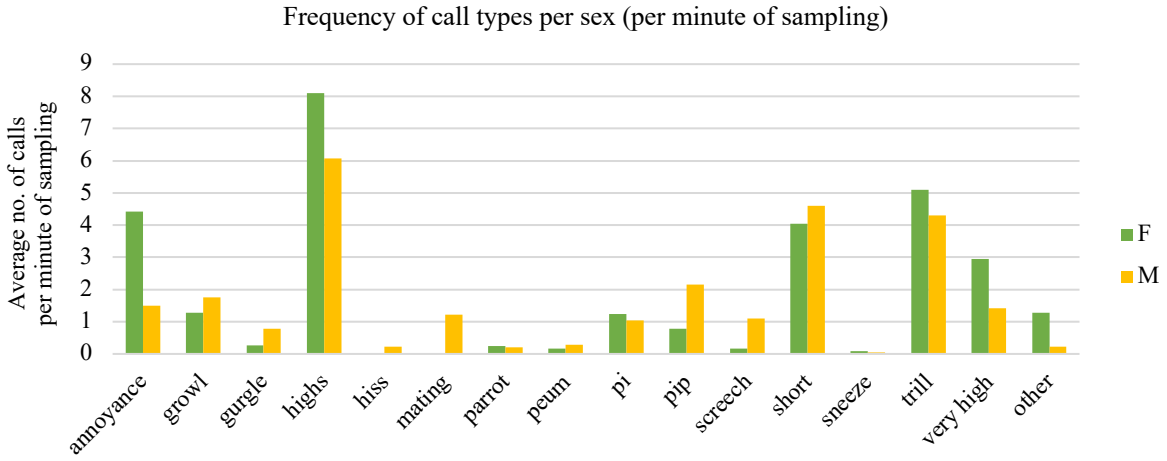

Fig. 3.6. Frequency of calls by sex for call types, corrected for the sample size of each individual.
Bar units show the average number of calls per minute of sampling. Green represents the frequency of females, yellow of males.

3.3 Acoustic analysis

3.3.1 Choice of acoustic parameters

The Principal Components Analysis applied to the 20 acoustic parameters surveyed revealed the ones most responsible for the variation present in the calls. The resulting first and second principal components accounted for 43.3% and 15.6% (resp.) of total variance, with high eigenvalues of 8.65 and 3.13, meaning that they contained the parameters relevant for the differentiation of calls. Although PC3 to 6 also had eigenvalues higher than 1, their contribution included all parameters, which would make the PCA redundant, and were consequently discarded. Since there were 20 variables put to test, the expected contribution was 5%, given by 1/20 = 5%. Therefore, variables with a contribution higher than this were considered explanatory of the variance contained in the PC. The parameters that fulfilled this requisite for PC1 and 2 and were non-colinear were used in the project's analysis, as displayed in Table 3.3 and Fig. 3.7 for PC1 e 2. These are SEM, duration, median, mean, Q25, bandwidth, average repetition rate, skewness, evenness, peak frequency, IQR. Even though peak frequency was colinear with bandwidth, it was included as well for purposes of description.

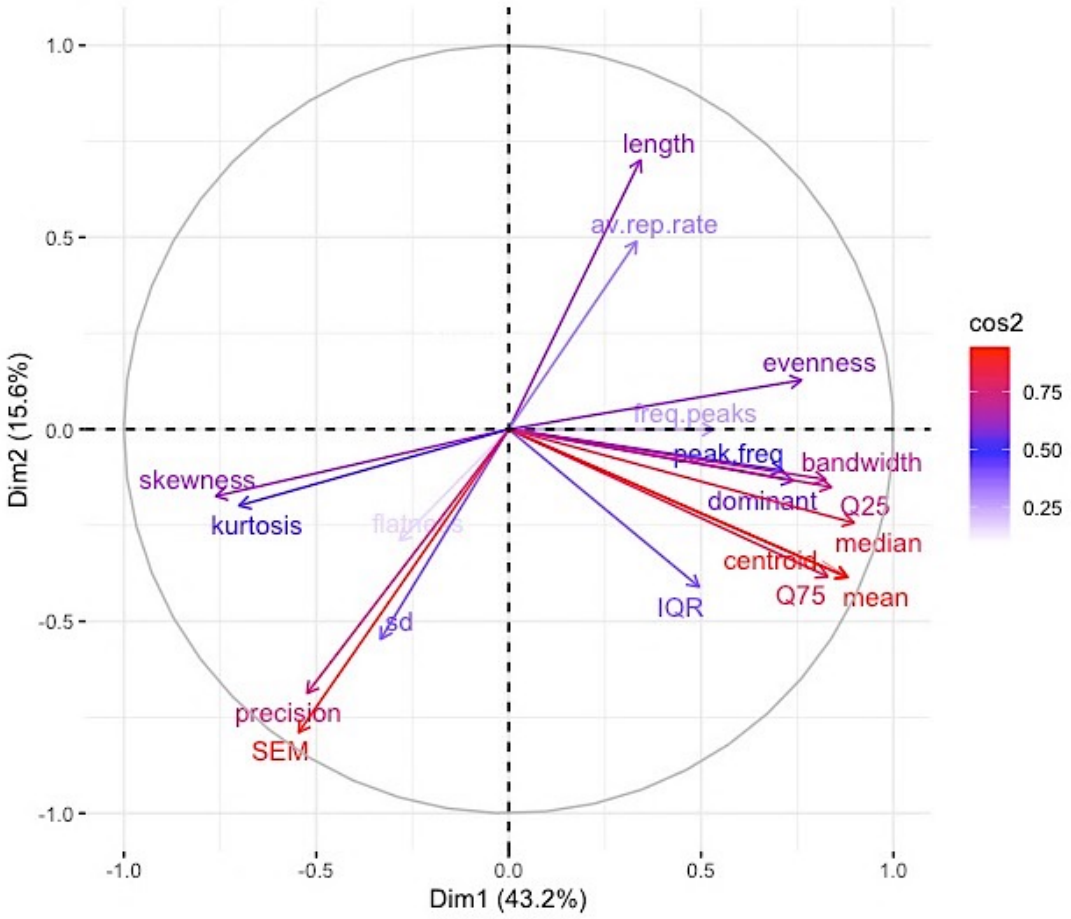

Fig. 3.7. Variable correlation biplot of Principal Components 1 and 2 (Dim) of the Principal Components.
Analysis explaining the variance of the acoustic parameters of all calls. PC1 is represented in the bottom axis and showing, PC2 in the left axis. The closer to the outer circumference the variables are, the more well represented they are in the PC, and more responsible for the variance explained by the PC. Cos2 represents the quality of representation for variables on the biplot; it is calculated as the squared variable coordinates on the plot. A higher cos2 is indicated in red, a lower cos2 is in light blue.

Table 3.3. Percentage contribution of relevant, non-colinear acoustic parameters to the variance represented by Principal Components 1 and 2, with contribution >5%. Peak frequency is colinear but included for purposes of description.

Principal Component 1	(eigen=8.65)
Median	9.32%
Mean	8.96%
Q25 (first quartile)	8.14%
Frequency bandwidth	7.85%
Skewness of frequency spectrum	6.70%
Evenness of frequency spectrum	6.70%
Peak frequency	5.87%

Principal Component 2	(eigen=3.13)
Standard error of frequency (SEM)	19.94%
Duration of call	15.73%
Average repetition rate	7.65%
IQR (interquartile range)	5.38%

3.3.2 Call type discrimination

Using the selected acoustic parameters as variables, the permuted Discriminant Function Analysis proved a correct assignment of the calls to the call types (p-value=0.001), further supporting a confident inclusion of the call types in the analysis. This is shown in the following test output:

Test factor: *call types*. Control factor: *sender*.
Nº cases: **897**
Nº correctly cross-classified cases **477.48**
Expected nº correctly cross-classified cases: **126.97**
Percentage of correctly cross-classified cases: **58.87%**
Expected percentage of correctly cross-classified cases: **15.53%**
P-value for cross-classification: **0.001**

3.4 Relationship between behaviours and vocalisations

The association between the frequency of behaviour categories and call types, analysed by Pearson's Chi-squared test with simulated p-value (based on 2000 replicates) was proven to be strong (X^2112 =1886, p-value = 0.0004998) (Fig. 3.9), even if with very high degrees of freedom. Several categories revealed to be positively associated with one or two call types, which indicated that these calls happened during these behavioural contexts more frequently than expected by pure chance. On the contrary, negative associations reveal that the call type will rarely be observed in that context. Relevant associations observed an absolute standardized residual value higher than 3.37. Noting some examples, annoyance and agonistic behaviours showed a standardized residual value of 17.814, and mating behaviours showed attraction to mating and hiss (st. res.= 26.846 and 11.947, resp.). .). Simultaneously, some behaviours exhibit negative associations with some call types, such feeding and very high pitched (st. res.= -7.648).

When applying the same test to a contingency table of the call types to the behavioural categories, there is again evidence against the independence of the variables (X^2588 = 4592.4, p-value = 0.000499) (Fig. 3.10) and reminiscent of the associations between the behavioural categories and the call types. The most important cells had an absolute standardized residual value higher than 3.8. The association

between mating and mating (st. res.= 36.170) and hiss and hiss were strong and positive (st. res.= 35.244). Both snapping and standing tall associate with the annoyance call (st. res.= 19.141 and 12.619, resp.) and alarm with both pip and screech (st. res.=10.859 and 5.025, resp.). On the other hand, short associated negatively with perching (st. res.=-5.151) and annoyance and very high pitched with chewing (st. res.= -5.126 and -4.818, resp.).

These associations, combined with the acoustic analyses of calls, results in a clearer and more complete description of the characteristics of vocal signals used in certain behavioural contexts (Table 6.2 of the Appendix).

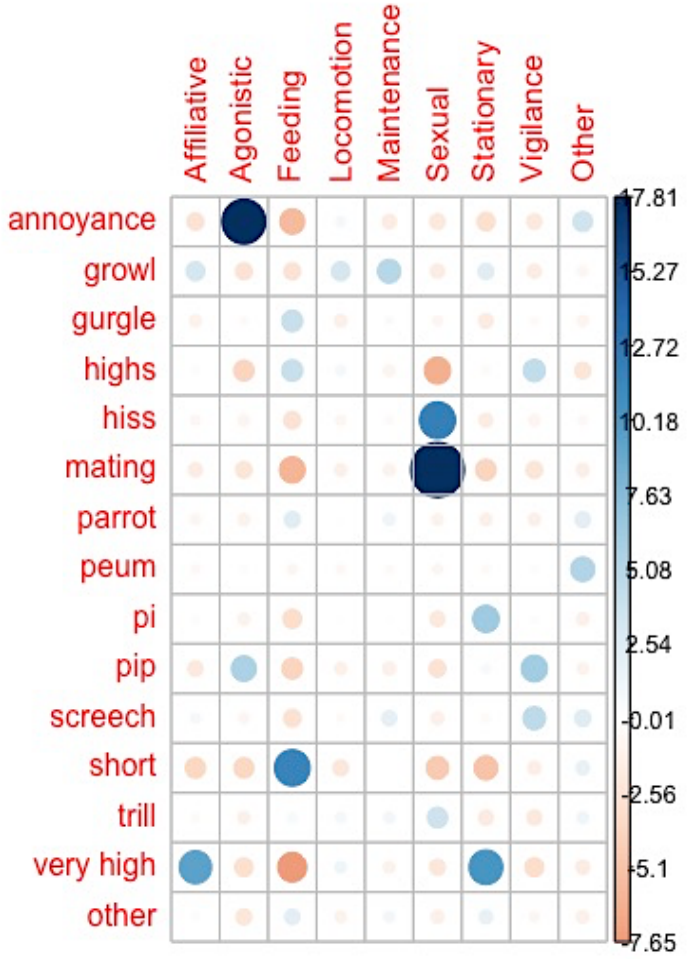

Fig. 3.8. Plot of standardised residuals of Pearson's chi-squared test for independence of behavioural categories and call types (X^2_{112} = 1886, p-value = 0.0004998)).
Positive residuals are in blue circles in the cells, specifying an attraction (positive association) between the corresponding row and column variables., while negative residuals are in red, which implies a repulsion (negative association).

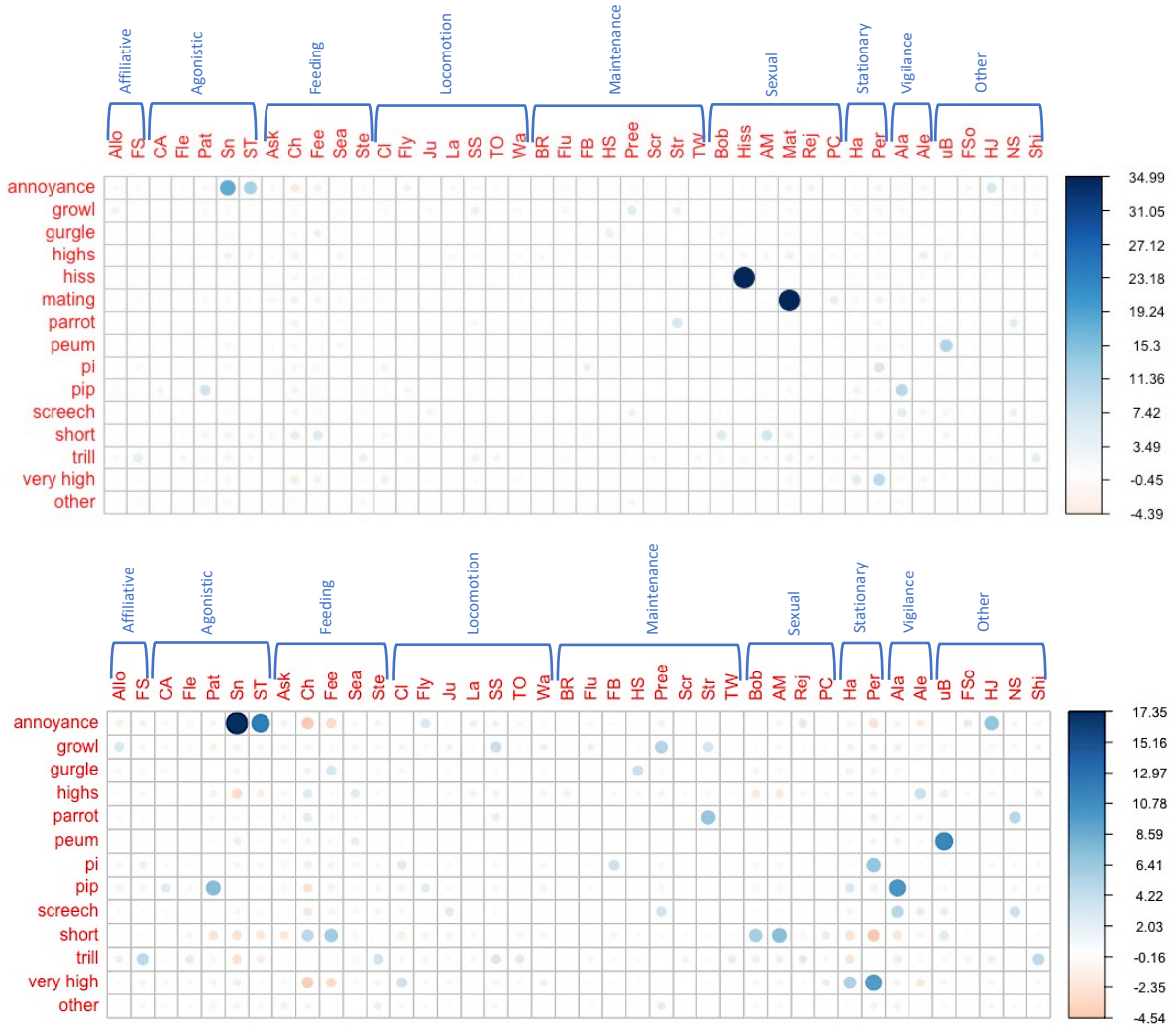

Fig. 3.9. Plots of standardised residuals of Pearson's chi-squared test for independence of behaviours and call types (X^2_{588} = 4592.4, p-value = 0.000499).

Above: all behaviours included. Below: Mating and Hissing behaviours and *mating* and *hissing* call types are removed for clearer analysis of the associations of lower value. Positive residuals are in blue circles in the cells, specifying an attraction (positive association) between the corresponding row and column variables., while negative residuals are in light red, which implies a repulsion (negative association).

3.5 Effect of call type and behavioural category on acoustic variation

The analysis of the acoustic parameters through GLMM with sender as the random effect showed that having call type as a fixed effect significantly explained the variation in all the acoustic parameters except bandwidth (X^2_{11}=19.578, p-value=0.515). On the other hand, behavioural category as fixed effect doesn't significantly affect the variations in any of the acoustic parameters, apart from bandwidth, which is only marginally significantly affected (X^2_8=15.927, p-value=0.0434) (Table 3.3).

Table 3.4. Results of Generalized Linear Mixed Model analysis with random slope and random intercept models for the 11 acoustic parameters, with either *call type* or *behavioural category* as fixed effects and sender as random effect for both tests. Significance codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.'.

	Call type		*Behavioural category*	
Acoustic parameters	**X^2_{11}**	**p-value**	**X^2_8**	**p-value**
SEM	34.946	**2.53e-04** ***	13.615	0.092
Duration	34.852	**2.6e-05** ***	5.812	0.668
Median	34.418	**3.09e-04** ***	13.027	0.111
Mean	35.558	**2.004e-04** ***	12.185	0.143
Q25	48.225	**1.302e-06** ***	10.697	0.223
Bandwidth	19.578	0.0515	15.927	**0.0434** *
Average repetition rate	44.371	**6.258e-06** ***	8.345	0.401
Skewness	56.373	**4.34e-08** ***	10.598	0.226
Evenness	89.519	**2.071e-14** ***	7.175	0.518
Peak frequency	39.786	**3.891e-05** ***	13.27	0.103
IQR	35.024	**2.455e-04** ***	10.737	0.217

3.6 Differences within the population

3.6.1 Sex

A pDFA with nested design shows that attributing the calls to the sex of the individuals through the variation in the acoustic parameters does not wield a significant result (p-value=0.581), as seen in the test output:

Test: *sex*. Control: *sender*.
Nº cases: **893**
Nº correctly cross-classified cases **372.23**
Expected nº correctly cross-classified cases: **372.94**
Percentage of correctly cross-classified cases: **51.91%**
Expected percentage of correctly cross-classified cases: **52.01%**
P-value for cross-classification: **0.523**

This result is corroborated both by Mann-Whitney tests on the acoustic parameters for the second most frequent call types, *high pitched* and *short*, all with a resulting p-value higher than 0.05, showing that there are no significant acoustic differences between the calls of each sex (Table 3.5).

Table 3.5. Significance of acoustic parameters to the differentiation between the calls of the two sexes for two call types. Results of Mann-Whitney tests for sex of the sender using the acoustic parameters in the *high pitched* and *short* call types, with test statistics value and p-value.
Significance codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.'.

	Sex			
Mann-Whitney tests	*High pitched*		*Short*	
Acoustic parameter	Z-score	p-value	Z-score	p-value
SEM	0.388	0.697	0.841	0.401
Duration	0.058	0.952	0.198	0.841
Median	0.791	0.430	0.992	0.322
Mean	0.636	0.522	0.815	0.412
Q25	0.798	0.424	-0.346	0.762
Bandwidth	0.431	0.667	0.450	0.653
Average repetition rate	-0.265	0.787	0.145	0.881
Skewness	0.462	0.646	0.194	0.849
Evenness	0.088	0.928	0.067	0.944
Peak frequency	0.304	0.764	0.323	0.749
IQR	-0.143	0.889	0.441	0.660

3.6.2 Individuals

The Kruskal-Wallis and one way analysis of means tests for differences between individuals found a significant effect in different parameters for the two call types analysed (Table 3.6).

In the *high pitched* calls, SEM was shown to be affected by differences in sender identity for both tests (KW: X^2_9=30.13, p-value=4.17e-04, one way: F=3.898, df=9, p-value=7.82e-04), as well as IQR (KW: X^2_9=19.621, p-value=0.0204, one way: F=2.809, df=9, p-value=0.00911).

For the *short* calls, one way analysis showed different results between the tests. While Kruskal-Wallis showed skewness as having a significant response from sender identity (X^2_7=14.648 , p-value=0.0408), one way analysis of means indicated median (F=3.778, df=7, p-value=0.0420) and peak frequency (F=12.300, df=7, p-value=0.00117) as being affected.

Table 3.6. Significance of acoustic parameters to the differentiation between the calls of different senders for 2 call types. Table of results for Kruskal-Wallis and one way analysis of means tests of differences in sender for each acoustic parameter, for the two most common call types: *high pitched* and *short*.
Significance codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.'

	Sender							
	High pitched				*Short*			
	Kruskal-Wallis		**One-way analysis of means (df=9)**		**Kruskal-Wallis**		**One-way analysis of means (df=7)**	
Acoustic parameter	X^2_9	p-value	F	p-value	X^2_7	p-value	F	p-value
SEM	30.13	**4.17e-04** ***	3.898	**7.82e-04** ***	8.698	0.275	1.101	0.453
Duration	14.67	0.100	1.447	0.193	11.536	0.117	0.686	0.684
Median	5,849	0.0755	0.575	0.811	12.847	0.0759	12.300	**0.00117** **
Mean	6.431	0.696	1.431	0.199	12.754	0.0783	2.915	0.068
Q25	6.694	0.669	1.360	0.229	10.017	0.188	2.494	0.121
Bandwidth	14.217	0.115	1.643	0.127	7.0033	0.429	1.932	0.200
Average repetition rate	15.032	0.0901	1.323	0.249	10.300	0.172	1.841	0.221
Skewness	12.82	0.171	3.898	0.0672	15.782	**0.0272 .**	2.572	0.09062
Evenness	10.712	0.115	1.534	0.161	5.224	0.632	0.730	0.655
Peak frequency	15.701	0.0734	1.431	0.199	12.236	0.0931	3.778	**0.0420** .
IQR	19.621	**0.0204 .**	2.809	**0.00911 ***	10.017	0.188	2.494	0.121

3.7 Particular case: F6 and the chattering lories

As mentioned before, F6 showed an affinity for human company. Whenever there was an open opportunity for her to get close to me without being run off by other rainbow lorikeets, she would readily come and vocalise to me, even bobbing her hear or performing the hissing motion (without the sound) of courtship behaviour, and would then carefully but steadily take the food from my fingers. Often, she would take it somewhere secluded to feed in peace, even if she had to climb all the way down to the ground.

On one fortunate occasion, on the 26th of January 2019, all other individuals were under the roof, close to the indoor area of the enclosure, and the feeding platform was vacant. F6 climbed on it and fed with no interruptions. When the food was finished, she asked for some, by walking excitedly close to the net and vocalising towards me. After a while I supplied some more fruit and left the camera recording while she fed and went for a walk around the other enclosures, stopping for some time by the two chattering lories of the Fugle Zoo (*Lorius garrula*) who were vocalising loudly.

Fig. 3.10. The two chattering lories (*Lorius garrulus)* of the Fugle Zoo.

In my time in the park, I observed this pair every now and then. They are medium sized, bigger that the rainbow lorikeets, and all red coloured. They were very skittish, moving extremely fast and readily interacting with me from the first day. I witness an interesting vocal repertoire from this pair, with at least 8 call types discerned by ear.

On that day, the lories again approached me when I got close, staring at me and excitedly jumping between the pole and the net (Fig. 3.11). they were vocalising repetitively with a high pitched, pulsed call, from before I arrived close to after I left back to the recording setup. As I got close to F6, she was feeding with her paw as usual and, as she chewed, she started vocalising as well, in a very similar call to the high pitched lory pulses.

In the superficial analysis of this fortunate recording, the spectrograms of the calls by the chattering lories and F6 look indeed visually similar, in a possible and surprising show of on-the-spot imitation. F6 managed to reproduce the calls with the same fundamental frequency, at around 2 kHz, and with similar harmonics, while having a slightly lower repetition rate (one pulse per 0.2 s, while the lories vocalised at around two pulses per 0.2 s).

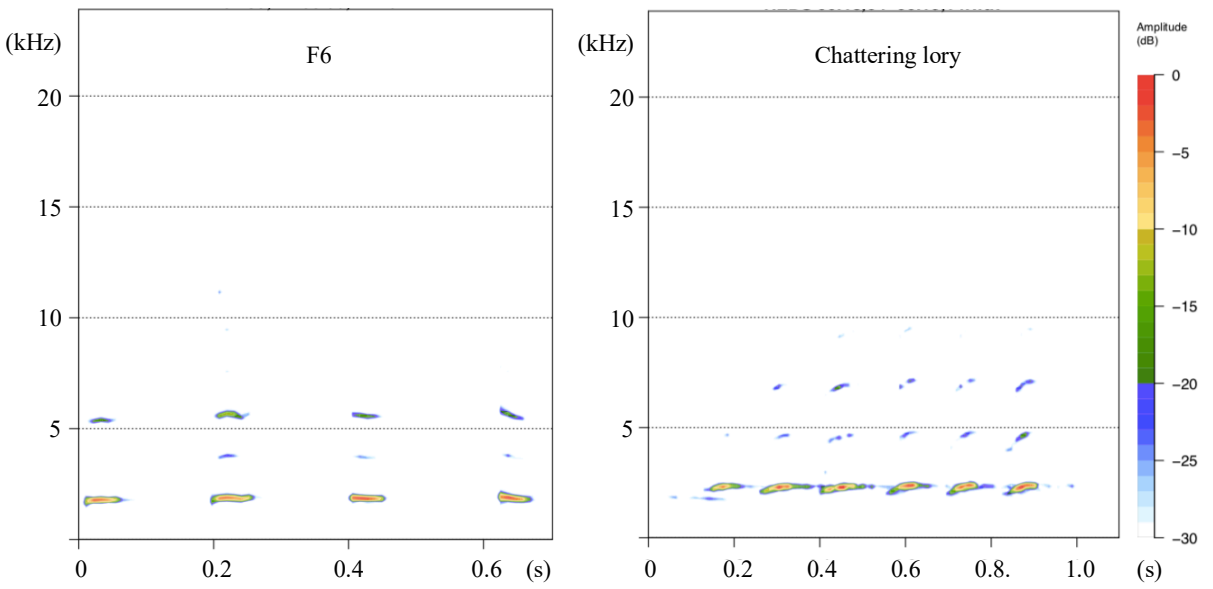

Fig. 3.11. Spectrograms of the calls of F6 after hearing the two chattering lories (*Lorius garrulus)* of the Fugle Zoo interacting with me.

– 4 –

DISCUSSION

4.1 Behaviour comparisons and relevance

The ethogram resulting from this research seems to be the most complete description of observed behaviours of the rainbow lorikeet presented so far, albeit from a captive population. While Higgins in 1999 and Serpell in 1989 described the behaviours of the species and the genus (respectively) with great care, there was some detail left to get to know still. Here, this was improved by having individual identification that allowed for the close following of the social dynamics.

The behaviours described in this captive-bred population and the categories they are inserted in seem to fit the overall knowledge of the wild flocks. Most of the time is spent feeding and looking for food, or just hanging or perching in a spot, with regular maintenance breaks and generally close to the mating partner (Fig. 3.1). While there were several feeding spots, mating pairs seemed to have a preference for a particular one and were almost always recorded in their respective platform.

It seems to be verifiable that the mating pair is indeed the basic unit of the social structure of the population (Chapman 2005), as the mated male and female were seen almost always together. This is coincident with Serpell's observations (1981) and seen in many other parrot species such as budgerigars, scaly-breasted lorikeets, canary-winged parakeets, cockatiels, among others (Brockway 1964, Trillmich 1976, Serpell 1981, Arrowood 1987, Spoon et al. 2004). The sharing of bond-strengthening affiliative behaviours, such as allopreening, happening only between pair mates and no other individuals is also prevalent in monogamous parrot species like white-tailed black cockatoos, spectacled parrolets, etc. (Saunders 1974. Garnetzke-Stollman & Franck 1991), as is the occurrence of these interactions outside of breeding season (Puerto Rican amazons (Snyder et al. 1987), galahs (Rowley 1990)). Since rainbow lorikeets mate whenever conditions are favorable (Higgins 1999), it is expected then to see these behaviours happening frequently and outside of mating context.

Rainbow lorikeets are also renowned for being very competitive, aggressively protecting feeding and nesting areas, both from conspecifics and other species, smaller or larger (Lamont & Burbidge 1996, Bruce 1973). This is part of what makes them an efficient invasive species (Chapple et al. 2013). This was obvious during recording, with the bonds and hierarchy becoming clear as the interactions between individuals added on, and evidenced by the differential frequencies of call types between individuals (Fig. 3.6). Both male and female participated in agonistic territorial encounters, especially mating partners as a cooperative interaction, just like yellow-naped amazons do for example (*Amazona auropalliata*, Wright & Dorin 2001). The diverse agonistic interactions seemed to reflect the hierarchical levels, and both males and females could hold high or low ranks (Table 3.1), as has been mentioned before in other parrot species such as blue-fronted amazons (*Amazona aestiva*) or monk parakeets (*Myiopsitta monachus*) (Matos et al. 2017, Hobson et al. 2014). It seems as well that the male and female of the mating pair hold the approximate same rank in the flock, as has been demonstrated in spectacled parrolets (Garnetzke-Stollman & Franck 1991). However, this issue could benefit from a more exact and exhaustive analysis on the hierarchical ranks. One method that has been suggested as the most acceptable one for classifications of hierarchy is the Elo-ratting (Albers & Vries 2001, Elo 1961, 1978). It takes into account the sequence of interactions of dominance between pairs of individuals and predicts the outcome of future interactions. It is, in fact, still widely used for chess players. This could easily be applicable to the Fugle Zoo population or other groups of interest over a long period of observations.

The population also showed indications of flock unity, especially during alarm situations, which were a frequent category of behaviour observed (Fig. 3.1). Whenever a cat would come to too close to the enclosure or even touched the net, or when the food car would come by, the whole group would react to it, synchronizing the vocalisations and flying around the space. M4 was, as described, often the first

to call out in alarm, while the other individuals remained for a little while in silent alert stance. This is concurrent with the existence of "sentries" that protect the flock while it feeds, as described by Higgins (1999).

In comparison with the previously published ethogram of the *Trichoglossus* genus on a group of 4 to 6 wild-caught individuals (Serpell 1989), some behaviours seem to have a correspondence. A behaviour described as very similar to the hissing display is called "hiss-up", with the wagging tongue and hissing sounds, that was however said to happen in agonistic encounters, while hissing was part of the courtship ritual. It can however be related to the standing tall behaviour in the agonistic category, since it includes the tall vertical posture and bowed head. Serpell also described one behaviour occurring in all studied species of *Trichoglossus* except *T. moluccanus* – "butting" – which seems very similar to the snapping presented here in the ethogram. In fact, the "butting" behaviour is said to happen in agonistic interactions, just like snapping. A behaviour that was not seen in *T. moluccanus* was named "alternated head-jerks", which could be directly associated with the ∩-bob; in Serpell's observations it was a movement made by two individuals, and at the Fugle Zoo one-third of responses of receivers to the ∩-bob was this same movement.

Differences in described behaviours could always be due to subjectivity of the observer, but it could also be possibly due to the different origin of the subjects, as well as a divergence in the functionality of behaviours due to cultural changes.

4.2 Mating behaviour

Here is now also presented the only detailed description of a mating ritual of rainbow lorikeets, since I found none in existing literature. In fact, the reproductive systems and behaviour of most species of parrots is still poorly studied, even if extremely interesting and diverse (Ekstrom et al. 2007) and useful for the success of conservation breeding programs (Seibert 2006). The mating behaviour itself is seldom described, and there are even accounts that were just recorded by accident (Birkhead et al. 2008).

It seems as though rainbow lorikeets mate by juxtaposition of the cloacas as in most bird species (King & McLelland 1981) and that the male has no penis. The courting of the male include movements seen in other species, such as bowing the head with open folded wings, as M3 did while *hissing* (seen in the cockatoo family (Zann 1965, Spoon 2002, Saunders 1974, Forshaw 1981), or the head bobbing in the *Agapornis* genus (Dilger 1960).

While parrots don't sing like songbirds do, there are recognized male calls in some species associated with courtship and mating, such as a warbling sound in budgerigars that is correlated with sperm production and ovarian stimulation (Brockway 1965).

Females of budgerigars are not often recorded performing courtship behaviours. Instead, they may remain still and even reject the advances of the male, sometimes aggressively, just as F3 did (Brockway 1964).

As for the duration of copulation, M3 and F3 mated from around one minute in one mount, which is within the range of studied parrot species. There is intraspecific variation, going from a minimum of 30 seconds in budgerigars to a maximum of 6 minutes in lovebirds (Seibert 2006). A difference between parrots and other birds that was also registered in M3 is that the male steps on the female's back rather than flying onto it (Dilger 1960, Hardy 1963, Brockway 1964, Eberhard 1998).

4.3 Vocal communication

Rainbow lorikeets' flocks are widely described as noisy (Chapman 2005), which could be an indication of the constant, complex and overlapping exchange of information between mates, with other individuals, between the whole group. This is expected, considering the dozens to thousands of individuals and interconnections happening at the same time, at all times. Males and females seem to be equally responsible for the ruckus, as they show the same call frequency (Fig. 3.3), which is concurrent with the equal ability of learning acoustic communication; this way, there is no bias towards a male-skewed ratio in vocalisations (Bradbury 2003).

The fact that 60 percent of calls could not have a receiver attributed is not a surprise, since they are significantly associated with the observed behaviours. Not all of these need a receiver to have functionality. Preening, for instance, serves the maintenance of the individual only and is associated with the *growl* vocalisation. Feeding and chewing have *short* and *high pitched* calls in strong association, and a lorikeet might feed alone or with his partner. Naturally, if the mating pair is the indeed the pillar of the social net in the group, the majority of receivers of directed calls were the partner.

A comparison could be made with the widely discussed *contact calls,* present in most parrots. These serve to countless purposes, from affecting social connections and coordinating movement and location of the flock during all kinds of activities, to communicating with individuals of other groups; they can either be loud or soft, used up close or at a distance, and even serve when there is no visual contact between individuals (Cortopassi & Bradbury 2006). I cannot assign one contact call to this population, since several of the identified and significantly distinct call types can serve these purposes, such as *very high pitched*, *short* and *trill* in bond-strengthening affiliative behaviour, to *short* calls during feeding, to *very high pitched* and *growl* during locomotion. Given the known complexity of parrot vocalisations, and the variety existing in contact calls in terms of acoustics and function (Cortopassi & Bradbury 2006, Adams et al. 2009), it could be a generalist term for a variety of calls vocalised within several species, and create difficulties in the comparison of different studies.

The repetition of pulses seems to be the norm for most call types in the repertoire, which can relate to the need to get the information encoded in the signal through. Adams et al. (2009) suggest that, while songbirds sing long songs, birds that use the shorter calls, such as parrots, repeat it so that the receiver can indeed seize its content.

4.4 Acoustic characteristics

4.4.1 *Variation between call types and behavioural contexts*

Given the fact that the attribution of calls to the call types has a measurable acoustic support, when disregarding interindividual variation (demonstrated by the pDFA test), it comes to no surprise that call types has a significant effect on the chosen acoustical parameters.

However, since there is an association between the frequencies of these call types and behavioural contexts, it was expected that these contexts would also have an effect on acoustic variation, thus giving functionality to the calls being used in each context. That was not the case (Table 3.4).

But functionality might just be the key to understanding why. Since some call types are used in more than one context (Fig. 3.9, Appendix 6.3), with some acoustic variation but not a significant one, this could lower the effect of context while keeping the differentiation between call types high. This might indicate that some call types have a more neutral or flexible function than others. As an origin for this, one could suggest that, in a group, the vocal signals could sometimes be recycled to serve various contexts, which could also contribute to the formation of dialects between populations.

4.4.2 *Individuality and sex*

The results in this population show that there are no significant differences due to sex of the sender the acoustics of calls, on any of the individually analysed parameters (Table 3.5). In terms of interindividual variation, the standard error of frequency mean (SEM) and interquartile range (IQR) of *high pitched* calls, the most used by the population, showed significant differences. On the other hand, in the *short* calls the differentiation has a low significance and is not coincidental between tests (Table 3.6).

This lack of significant variation between individuals contrasts directly with previous research in parrot calls, in which the acoustic characteristics of calls show differences according to the identity of the sender and encode this information to all receivers (Fisher & Wanker 2001, Thomsen et al. 2013). It was indeed a central prediction that did not come true. An interesting set of variables can explain this result: the individuals of this species with vocal learning abilities had lived in an unchanging social group and enclosure for 6 years. Just as it is necessary in the dynamic fission-fusion flocks in the wild – where group members can fluidly change – to quickly adapt to the dialect of the flock, there is evidence of convergence of calls within parrot groups with stable and stationary social links (Bradbury et al. 2001). The necessary cues coded in the significantly diverse signature calls of wild populations, that help mediate interactions with newcomers (Cortopassi & Bradbury 2006) is no longer necessary in a population that always roosts in the same place and has no visual obstructions to call identity. As is shown by studies done with captive individuals bred by different people, and that are housed together for the research period, it can start with imitation of calls in the mating pair to facilitate bonding, as quickly as in 3 weeks' time (Hille et al. 2000). Later it can be completed by group-level convergence, with widespread use of the same dominant call in 4 to 8 weeks (Farabaugh et al. 1994, Bartlett & Slater 1999). In addition, these facts don't diminish the importance of mediation of social dynamics, as seen in the functionality of calls (by association to behaviours). This similarity of acoustic characteristics seems, then, to be just one more proof of remarkable vocal learning skills, leading to their similarity of sound signals, and could be included in research over the social intelligence hypothesis (Dunbar 1998), with vocal convergence working towards social mediation of a functional group. The fact that there is some interindividual variation could be reminiscent of the different origins of the individuals in the Fugle Zoo population. Notably, variation in frequency values of different individuals, as is observed in the *high pitched* calls, has been shown, for instance, in spectacles parrolets and peach fronted conures (Fisher & Wanker 2001, Thomsen et al. 2013).

Since acoustic similarity is moreover equally shared between sexes, and there is considerable amount of communication and behavioural effort that is put into maintaining the bonds between mated partners, there can be a link to the relationship intelligence hypothesis. Further studies on the same population to verify the maintenance of mating pairs and how the relationship is cared for could lead into insight of what it takes to achieve this long-term commitment and connect it to necessary cognitive abilities.

4.5 Repertoire comparison

A previously published work on the vocal displays of captive rainbow lorikeets by the aforementioned Serpell classified 26 call types in 12 categories based on function, although without enough good-quality spectrograms to allow for visual comparisons (Serpell 1979). It could be a coincidence that this call type

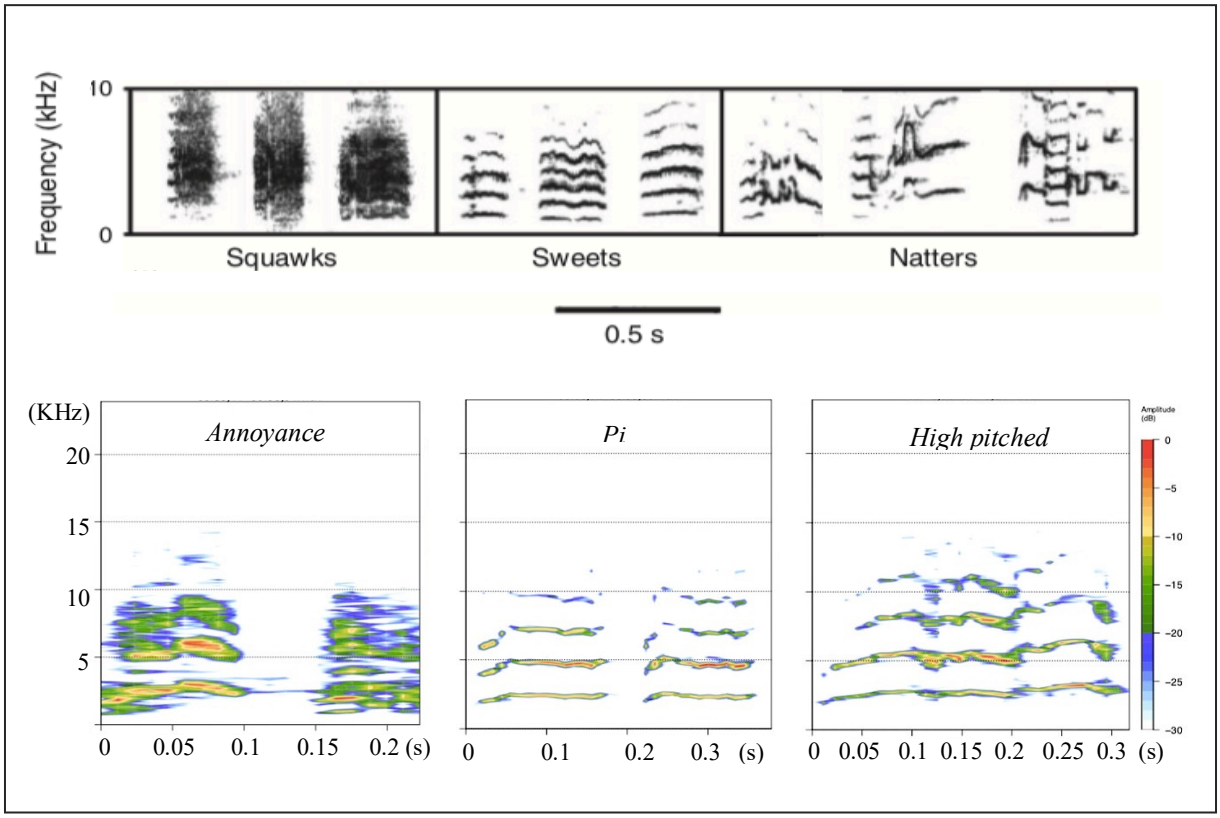

Fig. 4.1. Visual comparison of spectrograms of call types between two studies.
Above: spectrograms from the Perth population of rainbow lorikeets (by Baker 2014). Bellow: spectrograms of the Fugle Zoo population from this thesis project.

repertoire showed 12 call types as well. Many calls types described by Serpell and other authors happen at close distance between the female and male of the mating pair, as seen in the Fugle Zoo population.

A more recent study in rainbow lorikeets took inspiration from the calls identified by Serpell in naming the calls from the introduced population in Perth (Baker 2014). It mentions two types of contact calls uttered in series of pulses, that Baker named *squawks* and *sweets*. The first is more common and associated to agonistic contexts, while both happen frequently between a mating pair in flight. Another type of call described was *natter*, a word in Australian slang for idle talk or conversation, that was heard between the pair with low intensity. As can also be seen in their spectrograms (Fig. 4.1), the squawks could be directly related to the *annoyance* calls from the Fugle Zoo population, and the sweets to *pi*, due to their frequent pulse repetition and visual and contextual similarity. Natters is a frequency modulated call that could be related to the *high pitched* calls, for their modulation complexity and variety, as well as it being a call type almost exclusively directed to the mating partner or to no particular receiver.

Higgins (1999) also enunciated several characteristic calls of rainbow lorikeets together with his exhaustive study on wild populations. A protest call with a head movement witnessed when feeding sites were disturbed can be associated to the *pip* call uttered in alarm situations. A warble made by mating partners can encompass the *short*, *growl* and *gurgle* calls.

It is worth noting that differences between populations can be due to the development of dialects. The wild populations show significant differences in vocal signals between each other, even if geographically close (Baker 2014), which can and is likely to be the case for zoo populations and captive-bred individuals of the same species.

4.6 Prospects

The lack of more research on parrot behaviour and cognitive and vocal learning skills is not unjustified. Many practical constraints are caused by their large and dynamic foraging ranges, functioning camouflage in the high canopies, skittish behaviour, lack of sexual dimorphism, and the difficulty in tagging individuals for identification (Bradsbury & Balsby 2016). And, if we want to study natural abilities on these fast learners, using captive born or bred individuals can be tricky without a proper experimental design, since their behaviour is so easily "tainted" by the animals around them, such as us human researchers, due to imprinting.

One more aspect to consider is the possible neophobia that so many parrots exhibit. This can easily hinder research by delaying schedule, due to the long period of habituation that the experimental subjects will need to start interacting with or reacting neutrally novelties around them. Its important influence in behavioural data should not be ignored (Réale et al. 2007).

Luckily, rainbow lorikeets overcome some of these difficulties, with due interindividual variation. Their beaks are not strong enough to destroy metal rings for identification, in the new urban environments where they have roosted there are thousands of individuals, and they are easily spotted thanks to the rainbow plumage and loudness. Even more, they seem to be not very neophobic, as experienced in the Fugle Zoo population and shown by their ability to colonize new environments successfully. The degree of neophobia in a species has even been related to variations in foraging and morphological specialization, social learning and, through it, the social intelligence hypothesis (Humphrey 1976, Jolly 1988, Greenberg 1990, Byrne & Whiten 1997). This reveals an interesting dichotomy to further explore in these parrots, and possibly relate to the ecological intelligence hypothesis, which proposed a relationship between "big brains" with high cognitive skills and complex food distribution, feeding systems and adaptation to new environments (Sol et al. 2005, Rosati 2017). After all, rainbow lorikeets have highly specialized feeding morphology but are neophiliac and successful colonizers of new environments.

Furthermore, they are on the spectrum of invasive species, with populations living in close proximity to humans all over the main cities of Australia, as well as being popular exotic pets. This could offer a rare accessibility to parrots that flourish both in their natural range as well as in captivity or in (accidentally) introduced populations, which creates a very good basis for the study of population differentiation. Dialects, vocal characteristics, behaviour, evolution of cognition and language; these issues could be studied through the analysis of populations living in different continents, of individuals of varying origins, of groups with distinct numbers and dynamics, such as comparing the Fugle Zoo population with resident rainbow lorikeets in Sidney, for example. Maybe even long-term studies with permanent access to the focus subjects could be available.

Furthermore, since urban evolution is a very contemporary topic which is getting a lot of attention, *T. moluccanus* can be an interesting case study, with an emphasis on how an advanced cognition and a high degree of social learning may or may not cause a species to adapt fast rather than wait for transgenerational physiological changes. This may be especially relevant in comparison with other parrot species, who are failing at adapting to their changing environment, taking into account their long lifespan.

On a very practical note, these findings could help in the creation of programs for teaching important vocal and behavioural skills to soon-to-be reintroduced captive parrots. This can prove essential for a successful cultural assimilation in the wild populations (White et al. 2012, Wright 2017), and even increase the knowledge of caretakers and the welfare of captive individuals while they are living under human care, since it can create dynamic daily activities. The possibilities are appealing.

The interspecies mimicry that F6's case suggests could also offer exciting research on how an individual that is low in the hierarchy of a group might use vocal learning skills to gain feeding advantages from a third species involved (the human researcher). By mimicking the calls from other individuals that she saw getting attention, she then seems to have tried to use the same calls to get the same reward, in a behaviour similar to social learning and imitation (Bandura 1971). Although this was an isolated situation during these recordings, it is not a singular case happening in a captive parrot environment, as I've accounted from parrots in the Lisbon Zoo, and could be analysed in zoos throughout the world for an in-depth look into how social learning can happen between different species.

These are just some of many doors open to possible research and comparative studies, to deepen the knowledge on this species but not only. They could provide answers on themes such as parrot basic ecology, the influence of the human presence and interspecific learning, the evolution of dialects and ritualized behaviours from cultural differentiation, the abilities of vocal learning and mimicry, and ultimately the evolution of non-primate and general cognition, intelligence and language.

– 4 –

FINAL THOUGHTS

Further steps have now been taken in the understanding and knowledge we have of *Trichoglossus moluccanus*, the first Australian bird to be portrayed in a painting (Fig. 1.4). A parrot that shows indications of complex social dynamics in a small captive population and maintains mating pairs as the basis of the group web. Whose vocal communication seems to have evolved to a convergent acoustic stability while keeping interesting vocalisation diversity. We can now have a closer look at their behaviour, including courtship and mating, which adds on to the variety of this order of birds.

All these indications point to the convenience of rainbow lorikeets as good research subjects, not only for the species itself but for other parrots, in many scientific areas from ecology to cognition and evolution. Nevertheless, one more constraint described in parrot research is the allocation of funds from basic research to conservation efforts (Bradbury & Balsby 2016), to which I will not oppose. However, it is true that programs can only be made with knowledge if they are to be successful, and too many species of parrots dwindle on the possibility of extinction to take chances on their success. If it is in our power to succeed in maintaining healthy wild and captive populations, it seems only fair that we should get to know who we are dealing with. Knowing not just how the individuals can survive, but also how they can be included in the wild populations is of utmost relevance for highly social and vocal animals. Studies on vocal learning and efforts for their application in conservation programs can make the difference between success or failure of reintroductions (Groom et al. 2017), just like having a common language or studying the native one can make a world of difference for human translocations.

The same can be said for species that are now the opposite: thriving and coming into human-made environments. If we are to share the same space with new species, it seems natural that we learn how they work, so there can be a peaceful coexistence. This goes directly to the growing populations of rainbow lorikeets in Australia, but in a more and more humanized world these two cases are daily issues: some species are fading away, some are flourishing. Researching rainbow lorikeets can have an impact on both.

This project also turned out to be an invitation into a process that is becoming rare nowadays, in science and daily life. If you look through the dates of the mentioned literature, most descriptive research that was accessed is from the last century. There now seems to be, and we are told of, a shift on the goal (and funding) of research: to ask and answer questions that have a practical and profitable application. But there is a fascination in having the luxury to just watch, describe and share the beautiful and intricate ways of the beings around us. And how can we in fact understand them, our close neighbours, if we don’t stop and watch?

– 6 –

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– 7 –

APPENDIX

7.1 Ethogram of the Fugle Zoo population of rainbow lorikeets (*Trichoglossus moluccanus*), with descriptions of the behaviours

1) Affiliative behaviour

Allopreening **Allo**

This social behaviour is found across many bird species (Forsman & Wight 1979), and the rainbow lorikeets frequently preen each other, specifically when perched. With the experimental subjects, this behaviour happened exclusively between a mating couple. The head and neck were the main body parts that the birds took care of on their mate, since they are quite inaccessible during self-preening (Olsen & Joseph 2011).

Food sharing **FS**

When feeding as a couple, one of the mates may agree to share the piece of food it is feeding on with the mate, either if the piece of food is on the ground or already in the beak of the first lorikeet.

2) Agonistic behaviours

Chasing away **CA**

The territorially protective or competitive rainbow lorikeet will walk speedily or fly towards the invasive lorikeet, with an imposing body language.

Fleeing **Fle**

When threatened, a rainbow lorikeet might avoid the aggressive behaviour of another by fleeing, either by walking away, flying away or climbing or jumping up or down to a near enclosure structure.

Patrolling **Pat**

To defend its territory, a rainbow lorikeet will patrol the area with fast movements and a tall posture.

Snapping **Sn**

The aggressive rainbow lorikeet will snap its beak at the receiver, close to its head, with a fast and violent head motion.

Standing tall **ST**

The rainbow lorikeet will assume a threatening posture by making himself look bigger. It will stand vertical, lengthening the neck, fluffing the feathers while looking down at the lorikeet it is threatening.

3) Feeding

Asking **Ask**

If the fruit is visible to them outside the enclosure net, they rainbow lorikeets will vocalise to the human holding it, and/or in the direction of the fruit. They will move excitedly and restlessly.

Chewing **Ch**

After taking a small portion of food, the rainbow will spend a prolonged time chewing it and sucking on the juices. This is reminiscent of their most common food preference - flower nectar - in which they approach a flower and use their tongue to suck out the liquid.

Feeding **Fee**

Almost all the lorikeets nibble on food (in this case, fruit) while it rests on a surface, taking small pieces from it using the beak. They may also hold it in the beak, for example if perched on a surface that is not flat, and nibble on it like so. Only one lorikeet, F6, was observed using her foot to hold the food while nibbling on it, much like an amazon parrot or macaw would.

Searching **Sea**

The rainbow lorikeets of the Fugle Zoo seem to be very picky with the fruit they eat, many times taking their time choosing the ideal piece to feed on.

Stealing **Ste**

Specially between the mating couple, the rainbow lorikeets will often time take, or attempt to take, the piece of fruit the other one is feeding on, sometimes from inside the beak.

4) Locomotion

Climbing **Cl**

Climbing is a typical behaviour for both wild and captive psittacids (Smith 1971). It is very common to see the rainbow lorikeets climbing the net around their enclosure, and it is a comfortable resting surface for them. They climb upwards, downwards and sideways using the beak and both feet alternately, in a beak-foot-foot rhythm, hanging from the beak and then wrapping the toes around the net strings. Sideways there is an evident pendulum motion of the posterior body, with the beak hanging first in the direction of locomotion and the feet swinging further on before clasping the net. The lorikeets can climb quite fast, being very agile both with head facing up or down.

Flying **Fly**

Flight is used to move between enclosure structures that are either close or far away. The body of the rainbow lorikeets stays very stable while in the air, in a straight line from beak to tail, slightly oblique to the direction of flight with the belly side facing the destination for easy landing. The wings move up and down very fast, revealing flashes of colour from the plumage. Vocalisations are not frequent while in flight.

Jumping **Ju**

The rainbow lorikeets can give small jumps on a surface, raising either both feet at the same time or a one at a time in a syncopated jump. Bigger jumps may occur, between close-by surfaces of different levels, in which one to three wing strokes happen to allow for the necessary momentum.

Landing **La**

The landing is very firm, the feet are either planted quickly or wrap around the net and immediately the wings are folded on arrival. They may even be folded before touching the landing surface, so the movement is finished with a small fall towards the ground.

Side-stepping **SS**

When perched on a wooden pole, the rainbow lorikeets can side-step for short distances, moving one foot at a time with the one closer to the direction of movement moving first, and with the other foot steeping next to the first one, while maintaining the direction of the body.

Take-off **TO**

The rainbow lorikeets assume a tensed and low body position, close to the ground surface and parallel to it, with head pointing forward and wings folded closely to the body, before taking off in flight. Can

include one or two fast preparations, bringing the centre of mass down and up and down again before slightly jumping up and forward and opening to wings for flight.

Walking **Wa**

The rainbow lorikeets walk with one foot moving forward at a time, in a fast pace, with a stable body alignment, and it can go in any direction relative to the alignment of the body. The whole foot is planted firmly on the ground/surface, and the lorikeet can move forward very fast on short distances. The walk remains stable on the natural flooring of the enclosure as well as the wooden surfaces. If walking on a wooden cylindrical pole, the anterior toes face inward to better wrap the foot on the round surface, which results in a wobble of the posterior body.

5) Maintenance

Beak gapping **BG**

The rainbow lorikeet will open the beak, as if yawning, for a brief moment.

Beak rubbing **BR**

The bird rubs the sides of the beak against an edge or wooden pole, to clean off food scraps.

Defecation **De**

After raising its tail, the bird will rapidly excrete.

Fluffing **Flu**

In a common bird maintenance behaviour, frequent during preening, the rainbow lorikeet will erect all its feathers while building up the tension in the body, and then shiver the whole body vigorously, lowering the feathers back slowly to place. It allows for any loose feathers or down feathers to be throw away, and to rearrange the plumage in the right direction.

Foot biting **FB**

The bird will nibble on its foot, cleaning around the scales. It may also bite on the identification ring, quite insistently.

Head shake **HS**

To clean the beak, or throw away unwanted food, the rainbow lorikeet will shake its head very fast and make the piece of food fly away.

Preening **Pree**

As feathered animals, birds take care of their feathers' condition by preening, which takes up a large portion of their day (Delius 1988). They will use their beak to arrange the barbs along the shaft, nibbling from base to tip, of each feather individually, placing it correctly along the plumage direction, in every part of the body that the bird's flexibility will allow for, namely the breast, the mantle, the flanks, the tail and the wings. Since the head and neck are inaccessible for the beak, sometimes the bird will preen these feathers with one foot, slowly scratching the head (Nice 1959). It is essential for maintaining a functional and healthy coat, free of impurities and parasites (Moss 2015), and for removing loose feathers and allow for the replacement of new ones. Furthermore, these lorikeets oil their coat with the secretion from the uropygial gland, taking it with the beak from the lower back, in order to protect, lubricate and waterproof each feather (Lovette & Fitzpatrick 2016).

Scratching **Scr**

The rainbow lorikeet will scratch a body part vigorously with one foot. If it scratches the head, it will close its eyes to protect them from the claws.

Sneezing **Snz**

When rainbow lorikeets sneeze, they normally shake the head as well, and frequently sneeze more than once in a row.

Stretching **Str**

While perched, the rainbow lorikeets frequently extend one leg and one wing backwards, of the same side, while balancing on the opposite leg, slowly until full extension and then retracting in a relaxed manner.

Tail wagging **TW**

With a vertical posture, the rainbow lorikeet will wag the tail feathers quickly and shortly.

6) Sexual behaviours (listed in chronological order)

The full mating ritual, between F3 and M3, was recorded on the 2nd of February of 2019 at around 12h45. The mating pair was recorded perched in the pole next to the feeding platform. It preceded as follows:

- At time zero of the ritual, (**0m00s**), M3 and F3 start allopreening, changing frequently between groomer and receiver.
- At **03m58s**, M3 begins courtship, starting with bobbing, building up to hissing until F3 snaps at him, at 00:35. This courtship lasts for a couple of minutes, with M3 going through bobbing, hissing and attempted mounting and F3 *rejecting* him frequently, after which M3 starts the sequence again. At the end of each cicle, M3 steps further on F3's back.
- At **6m08s** M3 starts the last cycle of courting, with bobbing, hissing and attempted mounting, stepping on top of F3's back, and she doesn't reject him.
- At **6m20s** mating begins, and it lasts for around 1 minute. F3 is perched with a low body posture so that M3 can stand on her back.
- At **7m30s**, M3's body enters a state of tension with the final rub and freezes in place. This is the end of mating and the start of the *post-coital* period. After one second of inaction, F3 snaps at M3 with the ANNOYANCE call, to which he responds with the same call type and jumps off of her back and assumes a frozen, tense perched position on the pole, while F3 starts preening herself.
- M3 remains frozen until **7m52s**, when F3 interrupts preening, sidesteps close to M3 and resumes her grooming. At this moment, M3 bobs his head looking at F3 and sidesteps to her. Both come closer and closer to each other until at **8m19s** F3 starts allopreening M3. The male snaps immediately at her, to which she preens, and at **8m34s** he starts allopreening her. The two mates switch groomer and receiver for some time, until at **09m53s** they jump to the platform to feed, ending the ritual.

Allopreening **Allo**

Courtship

- **Bobbing Bob**

To initiate mating, the male engages in a courtship ritual, starting by coming very close to the female in a relaxed posture, with folded wings and sleek head feathers, accompanied by a fast bobbing up and down of the head.

- **Hissing Hiss**

After several head bobs, the male proceeds to open the bend of the wing back (keeping the wings closed down), displaying the colourful inner feathers, extends the neck while lowering the beak to the chest, and fluffs up the head feathers. He then keeps this posture while sliding the head from one side to the other and hissing towards the female, wagging his tongue in the mouth, eye-blazing (visible expansion of the orange irises (Serpell 1981)) and changing the weight from one foot to the other. There is approximately one hiss per second.

- **Attempted mounting AM**

Before copulation, the male will flap his wings very fast and simulate climbing onto the female's back, until he's finally accepted.

- **Rejection Rej**

Many times, during the courtship, the female rainbow lorikeet will reject the advances of the male, either by *snapping* at him, *sidestepping* away, *standing tall*, or simply *preening*.

Mating Mat

During copulation, the male finally climbs onto the female's lower back, with the help of very fast wing flapping, and proceeds to attempt to rub his cloaca with hers, carefully balancing on top of the female, flapping his wings for balance whenever necessary. He assumes a very hunched position, while aligning his body with the female's, and softly emits calls with each rub. The head balances increasingly with each rub.

Post-coital PC

After a certain period of copulation, the male will go rigid, tensing up, and freeze. He will jump off with the wings flapping, and perch very rigidly.

7) Stationary behaviours

This category describes the times for stillness, which are a big part of the day for these birds.

As some of the most frequent singular recorded behaviours (12.5% for perching and 5.3% for hanging), 17.8% of the total count of behaviours were stationary. This category is also associated with a great diversity of call types, with all being accounted for during these behaviours.

Hanging Ha

The rainbow lorikeets hang on the net in a very stable manner, with the toes wrapped on the net strings, one foot higher than the other, allowing for the beak and head to be free.

Perching Per

Often times, the rainbow lorikeets will be standing still, perched in a wooden pole, and very often right next to their partner. They keep the wings folded, the feet planted firmly and a vertical posture. It is the

way most of the time is spent. They may appear calm and relaxed, or more tense and alert, and/or attentive to the surroundings.

8) Vigilance

This category includes behaviours observed on the imminence of any threat coming close to the enclosure. These were most commonly cats of the Fugle Zoo and could also be a response to vigilance calls of the birds in surrounding enclosures.

Alarm Ala

One or more rainbow lorikeets may call out alarm vocalisations, frequently after being on alert, because of a disturbance around the enclosure, and it may cause a commotion in the group. Very common upon the approach of the park's resident cats, as well as the coming of the food car (brought by one of the park's caretakers). It is uttered with a tense, lowered body and frequently a fast head motion.

Alert Ale

At times, but particularly when something happens around the bird or in the surroundings of the enclosure, the rainbow lorikeets will stop their current action, tense up and stand slightly more vertical while looking around. It is a "contagious" behaviour, that is picked up very quickly from other rainbow lorikeets around.

9) Other behaviours

The behaviours in this category have no associated response, meaning that they lack a possible inference of function, or a similar behavioural description in literature. This can be due to lack of sampling or rarity of occurrence.

∩-bob ∩B

The rainbow lorikeets will move the head in a upside-down U shape (∩), going from one side to the other, often times coordinated with a vocalisation. It is observed with a body language of seeming excitement, although the receiver response is inconclusive as to its function: one third of responses was a ∩-bob and the remaining are neutral (stationary or feeding).

Foot shoving FSo

Without any negative consequences, a bird will use its foot to force distance from another one that is in close proximity. Recorded merely thrice and between F3 and M3.

Head jerk HJ

Some rainbow lorikeets were observed doing a very fast head motion from one side to the other when vocalising.

Neck stretching NS

The rainbow lorikeets will extend the neck while calling out and return to neutral neck position immediately after vocalising.

Shiver Shi

The bird will shiver its body, noticeably in the wing bends, as if nervous or excited. It happens almost exclusively directed towards another individual, but all responses are neutral, stationary behaviours.

7.2 Description of call types

The 12 call types found are diverse categories of calls, here generally described and associated with behavioural categories, with significance tested by chi-squared test. To the right, exemplary spectrograms of each call type are displayed, with different scales in the bottom axis representing time in seconds (Fig. 6.1).

1) Annoyance

This call type was first named after its frequent occurrence in behaviours of agonistic context. This correlation was verified to be true, with a high association between this call type and the category of agonistic behaviours (st. res.: 9.610). It contains harsh, broadband sounds (evenness: 0.875 ± 0.022), with only 19.17% of recordings containing harmonics. It is mostly composed of two short pulses (141 ± 46 ms), vocalised close together, and one with a higher peak frequency than the other, so that it sounds as if the pitch is going up or down from one pulse to the other. The frequency bandwidth values are the second highest of all call types (8.039 ± 1.746 kHz).

2) Growl

These are mainly quiet calls, with few, long-duration pulses (379 ± 159 ms), associated with maintenance behaviours (st. res.: 4.931). They have low mean frequency (1.684 ± 0.791 kHz) and peak frequency (1.683 ± 0.791 kHz). Their evenness is relatively high, at 0.858 ± 0.028, making them mainly inharmonic calls.

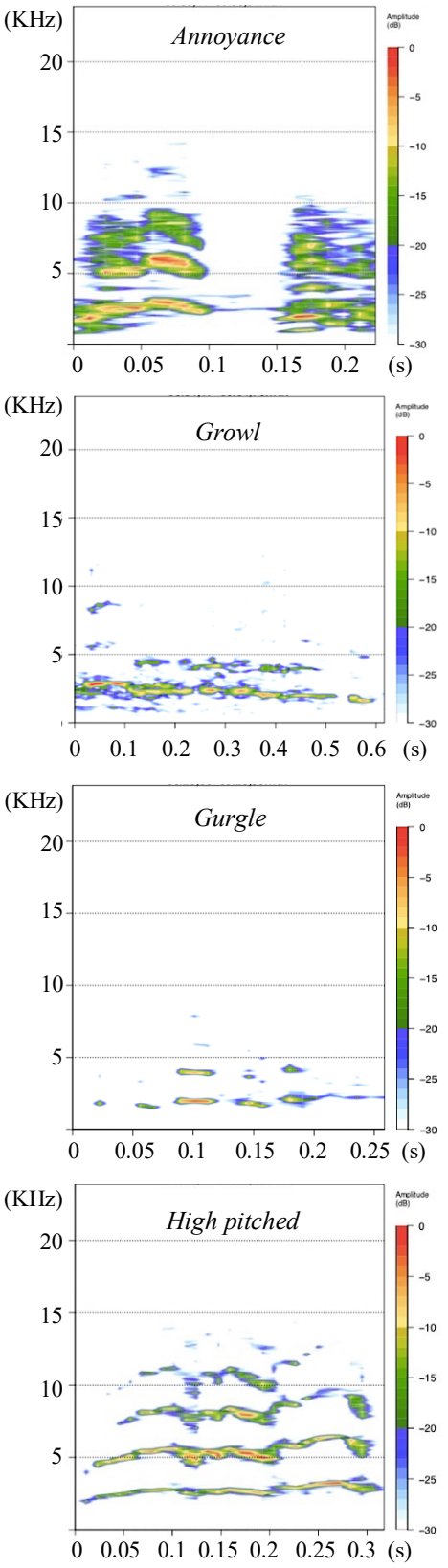
3) Gurgle

So named due to their similarity to the sound made when gurgling with water, these are quiet calls as well, made up of several short pulses (136 ± 167 ms) in a row. The *gurgle*'s peak frequency and mean frequency have similar and low values (1.683 ± 0.791 and 1.684 ± 0.791 kHz, resp.) They are scarcely recorded (30 calls) and are associated with a feeding context (st. res.: 3.997).

4) High pitched

This is a very diverse type of calls, and it was created to encompass varied vocalisations that sounded subjectively high pitched and with a frequency modulation with a modest slope, which could go up or down from beginning to end (in the example spectrogram, the frequency rises slightly during the call on fundamental and harmonics). This is confirmed by the high mean frequency (4.896 ± 0.940 kHz) and peak frequency (2.806 ± 1,064 kHz), even though the range of both acoustic parameters is big. Around half of the calls present a harmonic

Fig. 7.1. Exemplary spectrograms of call types. Left axis: frequency (kHz); bottom axis: time (s), right colour scale: relative amplitude. Obtained with Fourier-transformation Hanning windows, with 512 window length and 0% overlap. Continued from page 66 to 69.



series (58%). It is the most frequently recorded call type (25.5%) and is associated with the behaviour categories of feeding and vigilance (st. res.: 4.022 and 4.343, resp.).

5) Parrot

The *parrot* call type is so called due to its by-ear, subjective resemblance to a call made by amazon parrots. These calls, rare in the recordings (recorded 12 times), are gruff sounds, broadband (evenness: 0.826 ± 0.038), with calls consisting of one long pulse (251 ± 147 ms). Few of them contain a harmonic series (30%).

6) Peum

The *peum* are calls merely recorded 8 times, but from 3 different individuals – F6, F2 and M2. They contain one long pulse (321 ± 37 ms) with a distinct frequency modulation, going from a high to a low frequency in a smooth slope (evident in the example spectrogram), which results in a broad bandwidth (6.946 ± 1.102 kHz). Their evenness values are the lowest of all call types (0.120 ± 0.039). The name comes from a subjective translation of the heard sound into a human word.

7) Pi

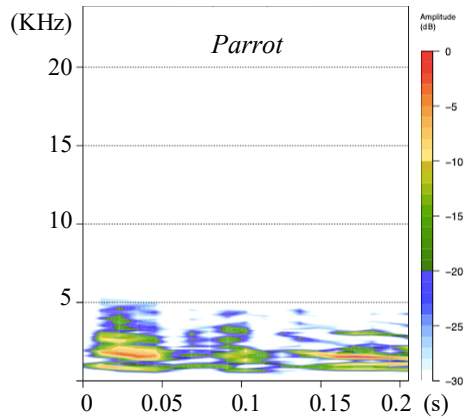
This high-pitched call type, with low variation in frequency (mean frequency: 5.285 ± 0.715 kHz), is characterized by calls with one to few pulses, a flat frequency modulation in the pulse (example spectrogram) and prevalent harmonic content (64% of *pi* calls, evenness: 0.129 ± 0.045).The pulses are not too short and the distance between them is not rushed; their duration varies little in the call type (184 ± 41). The peak frequency is maintained in the pulses of the same call. It is associated with the category of stationary behaviours (st. res.: 6.378).

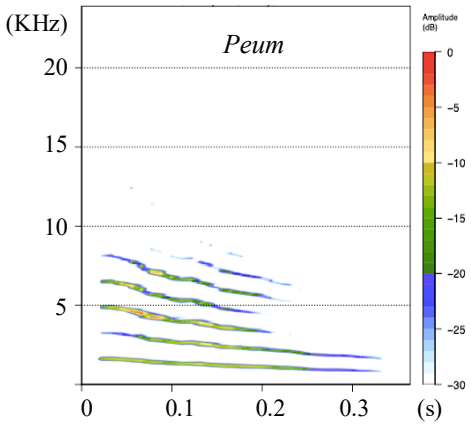
8) Pip

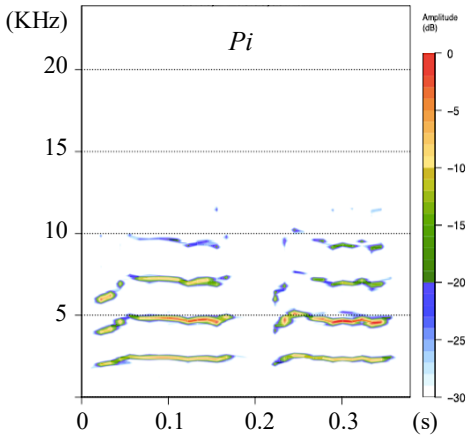
These are loud calls that were heard notably during alarm situations, specially upon the approach of a cat, making them associated with vigilance contexts as well as agonistic behaviours (st. res.: 6.206 and 5.647, resp.). They have short, uniform, back-to-back pulses (195 ± 41 ms), frequently in pairs or trios (1.6 ± 0.9 pulses per call) and sounding very similar to each other in the same call. They are relatively harsh-sounding pulses but with low evenness values (0.138 ± 0.025). The mean frequency bandwidth of *pip* is the highest of all call types (8.105 ± 1.302 kHz), as well as the peak frequency (5.205 ± 1.267 kHz).

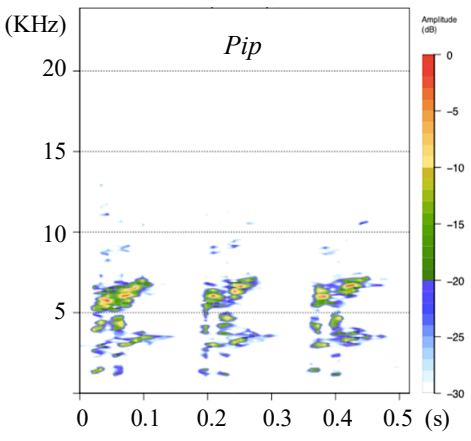
9) Screech

The screech calls are similar to high pitched ones but less melodic, sounding gruffer (75% of *screeches* lack harmonics)









although with low evenness (0.147 ± 0.022). Their frequency values (mean frequency: 5.551 ± 0.653 kHz, peak frequency: 3.192 ± 1.285 kHz) are in the higher ranges of the *high pitched* calls, and they have merely one long pulse (350 ± 134 ms). Even though they are relatively scarce, with 25 recordings only, they have an association to vigilance behaviours (st residuals: 4.620).

10) Short

This call type is, again, a very diverse umbrella of short calls (107 ± 48 ms) with very few pulses (maximum of 3 pulses per call). They can be louder or quieter and show a low peak frequency (1.830 ± 0.609 kHz) but higher mean frequency values (4.088 ± 0.776 kHz). In addition, they are very harmonic calls, with 79.2% prevalence of harmonics series, sometimes with only one or two harmonics. *Short* calls are the second most recorded (17.8%) and are associated with feeding (st. res.: 11.677).

11) Trill

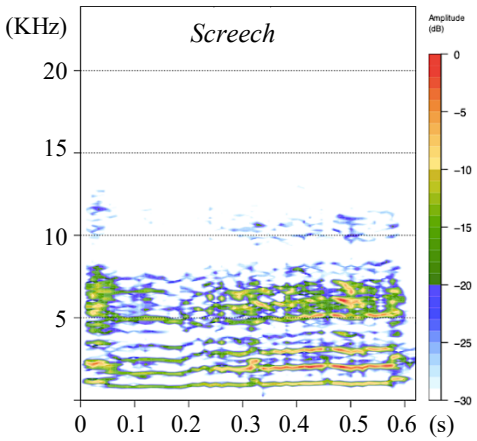
A commonly heard vocalisation from birds, the *trills* are bursts of very short pulses in a row (pulse duration: 71 ± 31 ms), up to 17 pulses in these short-duration calls (291 ± 111ms), in a skillful display of amplitude modulation. Each call can be composed of merely the short trills (pictured in the example spectrogram) or also have an ending with a longer pulse. The peak frequency values are around half of the mean frequency values (2.307 ± 0.777 and 4.684 ± 0.781 kHz, resp.), and the evenness values are low (0.166 ± 0.052), with around half of trill calls containing harmonic series (55.1%). It shows no specific association to a behaviour category.

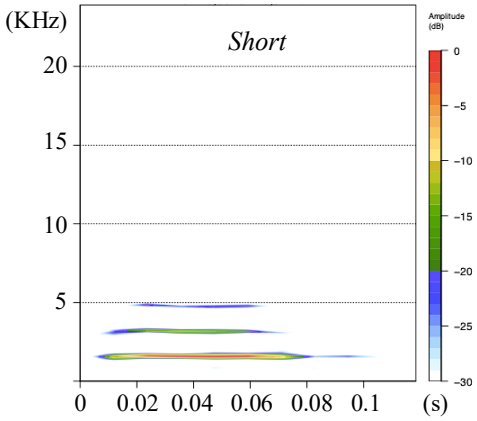
12) Very high pitched

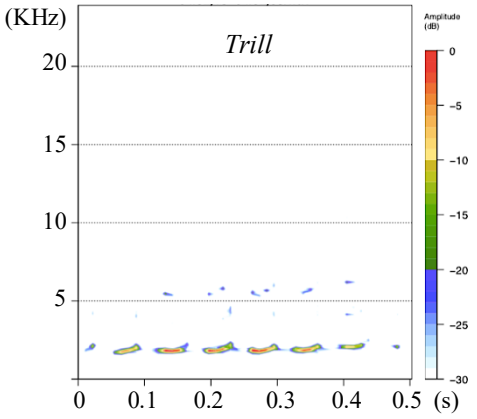
The *very high pitched* calls were named so because of the pain they caused in the eardrum when hearing them through headphones in the recordings. They have indeed the highest mean frequency of all call types (6.115 ± 0.752 kHz). Even if painful, they have a very melodic sound, with 80% of these calls containing harmonic series, and show complex and diverse frequency modulations in one-pulsed calls (only one was found to have 2 pulses). Their evenness values are the second lowest (0.122 ± 0.025), nearing them to pure tones. This call type is strongly associated with affiliative behaviours (st. res.: 9.610).

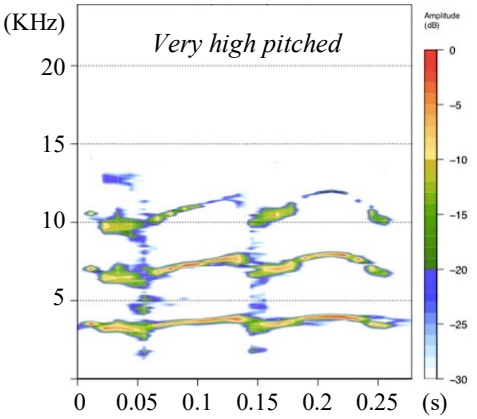
13) Other

This was the category where all the rare call types were grouped. It included the *opera*, a call of three pulses rising in frequency just like an opera singer might do, *pierce*, a single pulse with only a fundamental frequency, *whistle*, resembling a flirty catcall









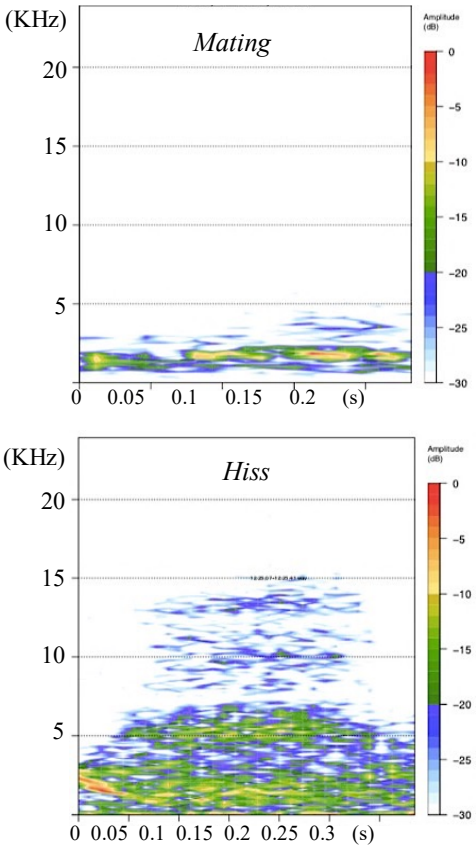
whistle, *scream*, a harsh-sounding short pulse with a fundamental and one harmonic, and *telephone*, a very fast trill that sounded like a telephone ring. The two other call types that were analysed were:

a. Mating

The mating growl was isolated for its specific occurrence during the one event of mating recorded, and was vocalised by M3. It is a very soft growl, emitted with every rub of the cloaca during mating and twice during the post-coital phase.

b. Hiss

The hiss is more of a mechanically produced sound than a vocalisation, since it is an exhalation made with the beak open and the tongue wagging, while slowly bobbing the head from side to side in synchrony. It was made during courtship by M3.



7.3 Acoustic characterization of vocal repertoire

Table 7.1. Summary of acoustic characterization for each of the 12 call types. On the left column is the minimum and maximum of the parameter values, on the right column is the mean and standard deviation of the parameter values. Continued from page 70 to page 72.

	Annoyance	
	Max - Min	Mean ± st. dev.
Pulses	1 – 6	1 ± 1,056
Pulse duration (ms)	231 – 636	141 ± 46
Call duration (ms)	53 – 1189	253 ± 200
Frequency bandwidth (kHz)	3.716 – 11,077	8.039 ± 1.746
Peak frequency (kHz)	0.844 – 8.156	3.162 ± 1.438
Frequency mean (kHz)	3.235 – 7.094	3.162 ± 0.795
Evenness	0.780 – 0.912	0.875 ± 0.022

	Growl	
	Max - Min	Mean ± st. dev.
Pulses	1 – 3	1.1 ± 0.4
Pulse duration (ms)	118 – 873	379 ± 159
Call duration (ms)	118 – 873	395 ± 151
Frequency bandwidth (kHz)	1.805 – 10.778	5.221 ± 1.992
Peak frequency (kHz)	0.750 – 10.776	1.683 ± 0.791
Frequency mean (kHz)	0.750 – 3.937	1.684 ± 0.791
Evenness	0.790 – 0.913	0.85 ± 0.028

	Gurgle	
	Max - Min	Mean ± st. dev.
Pulses	1 – 8	2.9 ± 2.3
Pulse duration (ms)	36 – 565	136 ± 167
Call duration (ms)	134 – 579	284 ± 141
Frequency bandwidth (kHz)	1.676 – 9.683	4.520 ± 2.174
Peak frequency (kHz)	1,031 – 3.188	1.969 ± 0.463
Frequency mean (kHz)	2.690 – 5.207	3.861 ± 0.654
Evenness	0.784 – 0.888	0.840 ± 0.027

	High pitched	
	Max - Min	Mean ± st. dev.
Pulses	1 – 6	1.2 ± 0.7
Pulse duration (ms)	60 – 757	269 ± 90
Call duration (ms)	111 – 757	288 ± 81
Frequency bandwidth (kHz)	0.195 – 10.571	5.602 ± 2.163
Peak frequency (kHz)	1,082 – 7.367	2.806 ± 1,064

Frequency mean (kHz)	2.634 – 7.361	4.896 ± 0.940
Evenness	0.688 – 0.899	0.834 ± 0.032

	Parrot	
	Max - Min	Mean ± st. dev.
Pulses	1	1 ± 0
Pulse duration (ms)	91 – 535	251 ± 147
Call duration (ms)	91 – 535	251 ± 147
Frequency bandwidth (kHz)	1.690 – 6.867	4.277 ± 1.505
Peak frequency (kHz)	0.769 – 3.093	1.789 ± 0.639
Frequency mean (kHz)	2.795 – 3.953	3.422 ± 0.473
Evenness	0.760 – 0.875	0.826 ± 0.038

	Peum	
	Max - Min	Mean ± st. dev.
Pulses	1	1 ± 0
Pulse duration (ms)	261 – 364	321 ± 37
Call duration (ms)	261 – 364	321 ± 37
Frequency bandwidth (kHz)	5.105 – 8.280	6.946 ± 1.102
Peak frequency (kHz)	1.330 – 4.057	3.047 ± 0.831
Frequency mean (kHz)	3.785 – 4.966	4.383 ± 0.442
Evenness	0.074 – 0.194	0.120 ± 0.039

	Pi	
	Max - Min	Mean ± st. dev.
Pulses	1 – 6	1.5 ± 1,0
Pulse duration (ms)	130 - 325	184 ± 41
Call duration (ms)	155 – 1390	306 ± 259
Frequency bandwidth (kHz)	2.762 – 9.541	5.975 ± 1.806
Peak frequency (kHz)	2.213 – 5.152	2.504 ± 0.931
Frequency mean (kHz)	3.778 – 6.906	5.285 ± 0.715
Evenness	0.018 – 0.258	0.129 ± 0.045

	Pip	
	Max - Min	Mean ± st. dev.
Pulses	1 – 4	1.6 ± 0.9
Pulse duration (ms)	106 – 223	195 ± 41
Call duration (ms)	100 – 674	275 ± 163
Frequency bandwidth (kHz)	4.935 – 11.338	8.105 ± 1.302
Peak frequency (kHz)	2.819 – 11.338	5.205 ± 1.267
Frequency mean (kHz)	4.794 – 6.888	5.901 ± 0.482

Evenness	0.085 – 0.193	0.138 ± 0.025

	Screech	
	Max - Min	Mean ± st. dev.
Pulses	1 – 1	1 ± 0
Pulse duration (ms)	231 – 636	350 ± 134
Call duration (ms)	231 – 635	350 ± 134
Frequency bandwidth (kHz)	6.371 – 10.566	7.987 ± 1.591
Peak frequency (kHz)	1.821 – 4.503	3.192 ± 1.285
Frequency mean (kHz)	4.460 – 6.317	5.551 ± 0.653
Evenness	0.112 – 0.190	0.147 ± 0.022

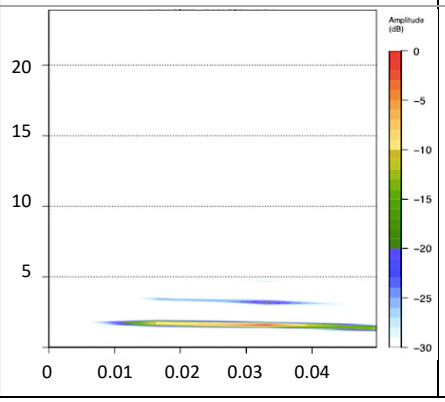
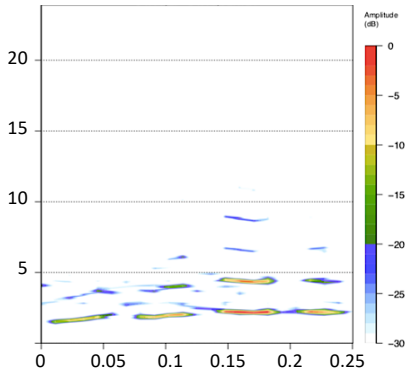
	Short	
	Max - Min	Mean ± st. dev.
Pulses	1 – 3	1.1 ± 0.3
Pulse duration (ms)	32 – 396	101 ± 44
Call duration (ms)	32 – 396	107 ± 48
Frequency bandwidth (kHz)	0.136 – 10.455	3.239 ± 1.902
Peak frequency (kHz)	1,096 – 4.896	1.830 ± 0.609
Frequency mean (kHz)	2.695 – 6.512	4.088 ± 0.776
Evenness	0.643 – 0.892	0.768 ± 0.045

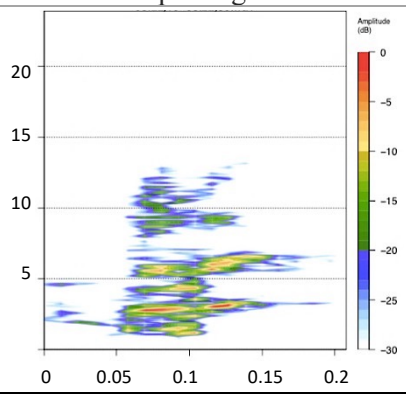
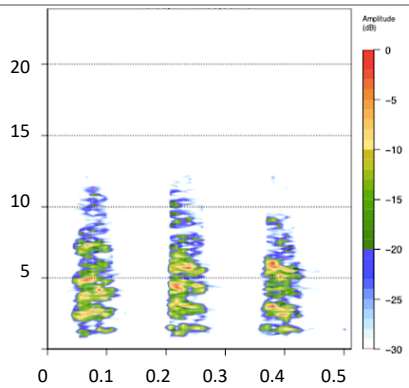
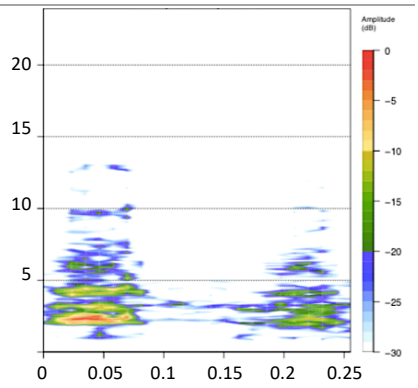
	Trill	
	Max - Min	Mean ± st. dev.
Pulses	2 – 17	4.6 ± 2.3
Pulse duration (ms)	34 – 228	71 ± 31
Call duration (ms)	99 – 713	291 ± 111
Frequency bandwidth (kHz)	0.366 – 10.139	5.018 ± 2.026
Peak frequency (kHz)	1.304 – 4.949	2.307 ± 0.777
Frequency mean (kHz)	3.262 – 6.186	4.684 ± 0.781
Evenness	0.090 – 0.428	0.166 ± 0.052

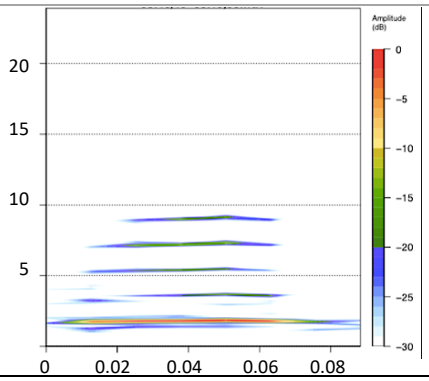
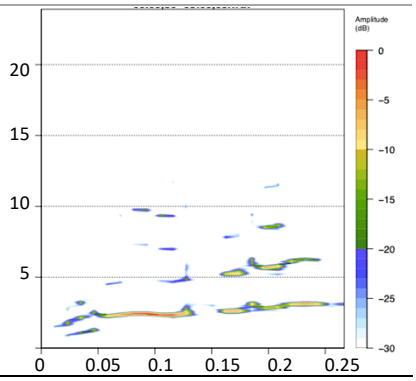
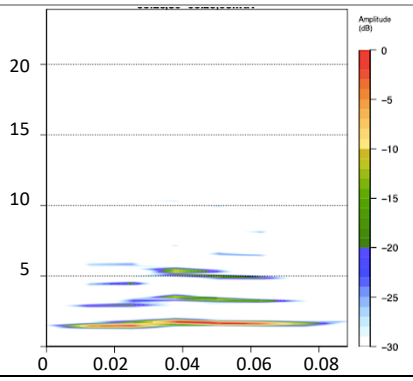
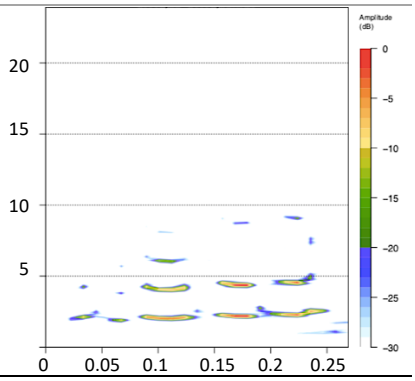
	Very high pitched	
	Max - Min	Mean ± st. dev.
Pulses	1 – 2	1,0 ± 0.1
Pulse duration (ms)	92 – 594	296 ± 90
Call duration (ms)	116 – 594	297 ± 1963
Frequency bandwidth (kHz)	1.542 – 9.712	5.919 ± 1.963
Peak frequency (kHz)	2.964 – 7.213	3.977 ± 0.933
Frequency mean (kHz)	4.194 – 7.370	6.115 ± 0.752
Evenness	0.083 – 0.177	0.122 ± 0.025

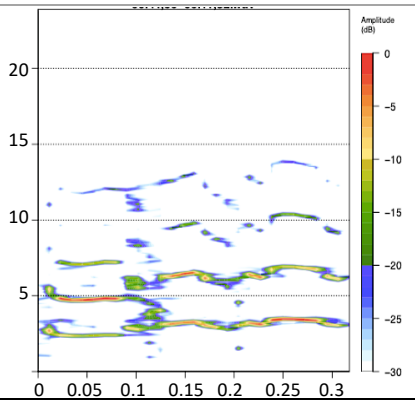
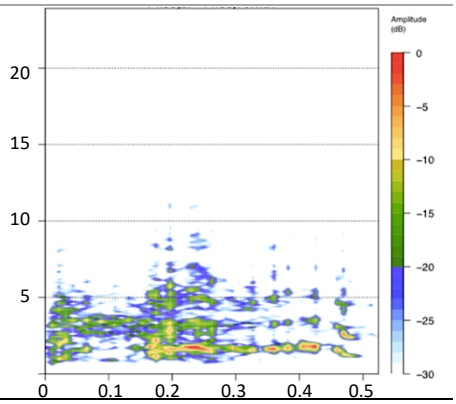
7.4 Description of the characteristics of vocal signals used in the 9 identified behavioural contexts

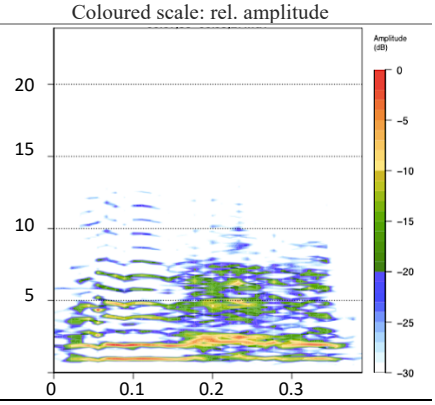
Table 7.2. Associations between behaviour categories, behaviours and call types, with respective acoustic characterization and spectrograms of calls used within the behaviours. Continued from page 73 to page 79.

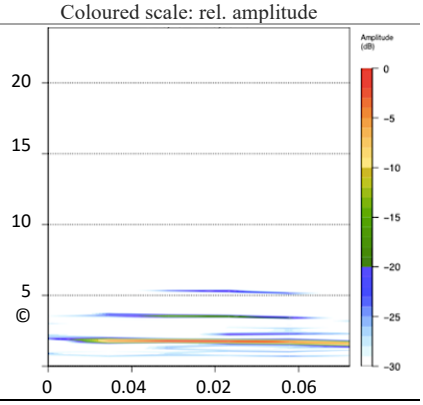
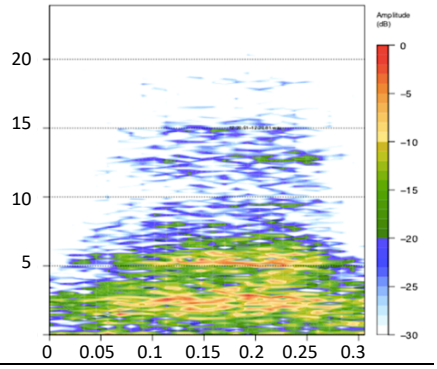
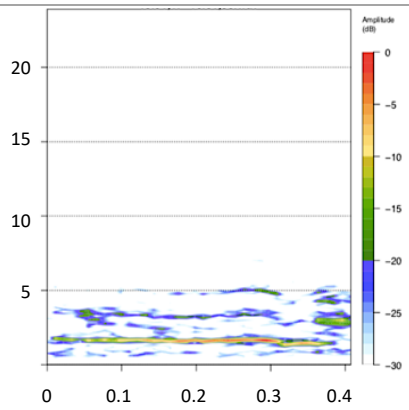
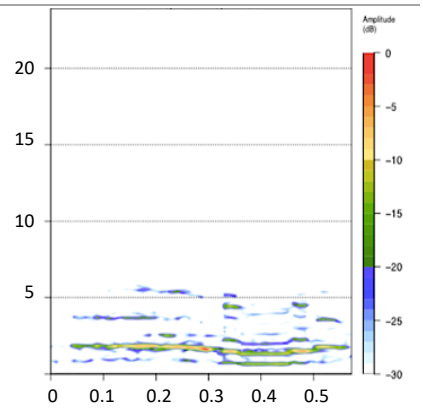
Behaviour category *Associated call type*	**Affiliative behaviour** *Very high pitched*	
Behaviour *Call type*	**Bobbing** *Short*	**Food sharing** *Trill*
Rel. freq. of call type in behaviour	81.3%	60%
Mean no. pulses per call	1 ± 0	3.0 ± 1
Mean duration (ms)	63 ± 8	209 ± 41
Bandwidth (kHz)	1.705 ± 1.134	3.875 ± 1.193
Peak frequency (kHz)	1.426 ± 0.206	2.011 ± 0.194
Mean frequency (kHz)	3.787 ± 0.465	3.934 ± 0.303
Spectrogram (Frequency (kHz) / Time (s)) Coloured scale: rel. amplitude		

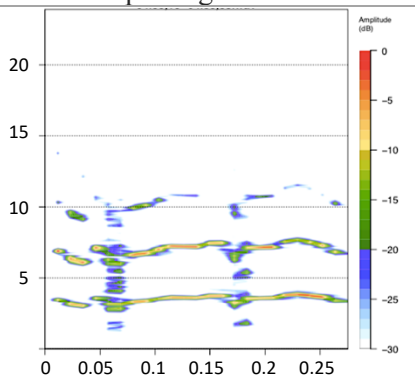
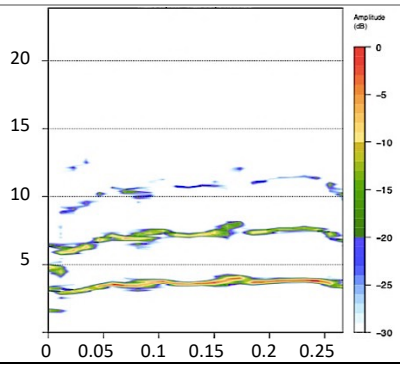
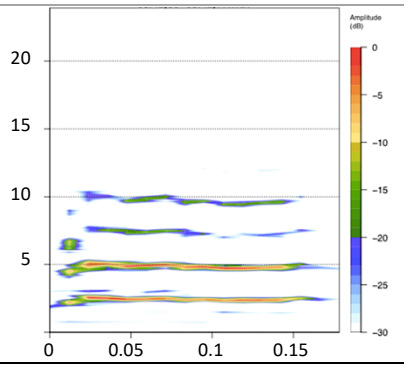
Behaviour category *Associated call type*	**Agonistic behaviour** *Annoyance*, *Pip*	
Behaviour *Call type*	**Patrolling** *Pip*	Spectrogram
Rel. freq. of call type in behaviour	32.6%	
Mean no. pulses per call	1.8 ± 1.2	
Mean duration (ms)	290 ± 212	
Bandwidth (kHz)	7.787 ± 1.706	
Peak frequency (kHz)	3.821 ± 1.162	
Mean frequency (kHz)	5.695 ± 0.522	
Behaviour *Call type*	**Snapping** *Annoyance*	**Standing tall** *Annoyance*
Rel. freq. of call type in behaviour	81.3%	60%
Mean no. pulses per call	2.3 ± 1.2	1.7 ± 0.8
Mean duration (ms)	349 ± 230	252 ± 139
Bandwidth (kHz)	7.804 ± 1.764	080 ± 1.265
Peak frequency (kHz)	2.860 ± 1.247	3.108 ± 1.485
Mean frequency (kHz)	5.008 ± 0.701	5.698 ± 0.468
Spectrogram (Frequency (kHz) / Time (s)) Coloured scale: rel. amplitude		

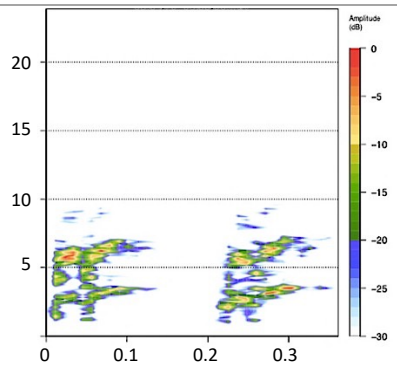
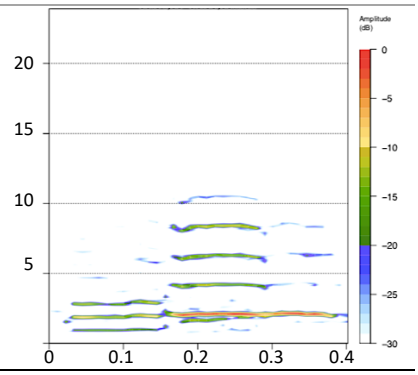
Behaviour category *Associated call type*	**Feeding behaviours** *Short*	
Behaviour *Call type*	**Chewing** *Short*	*High pitched*
Rel. freq. of call type in behaviour	30.5%	34.2%
Mean no. pulses per call	1.1 ± 0.3	1.1 ± 0.3
Mean duration (ms)	106 ± 37	286 ± 77
Bandwidth (kHz)	3.780 ± 2.136	5.953 ± 2.424
Peak frequency (kHz)	1.862 ± 0.561	2.727 ± 1.140
Mean frequency (kHz)	4.280 ± 0.895	5.065 ± 0.988
Spectrogram (Frequency (kHz) / Time (s)) Coloured scale: rel. amplitude		
Behaviour *Call type*	**Feeding** *Short*	**Stealing** *Trill*
Rel. freq. of call type in behaviour	36.9%	45.5%
Mean no. pulses per call	1,0 ± 0.2	4.3 ± 1,0
Mean duration (ms)	112 ± 63	278 ± 96
Bandwidth (kHz)	3.040 ± 1.636	3.790 ± 0.836
Peak frequency (kHz)	1.790 ± 0.405	2.225 ± 0.116
Mean frequency (kHz)	3.936 ± 0.687	4.768 ± 0.722
Spectrogram (Frequency (kHz) / Time (s)) Coloured scale: rel. amplitude		

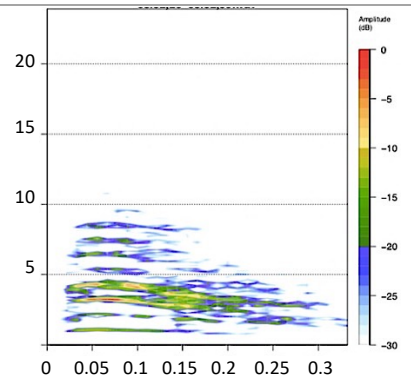
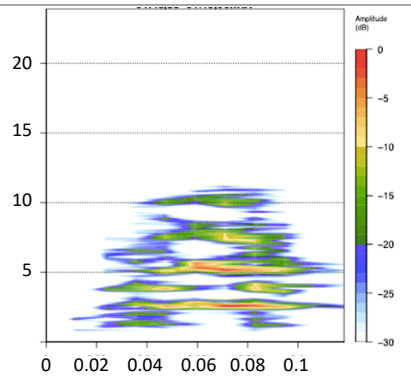
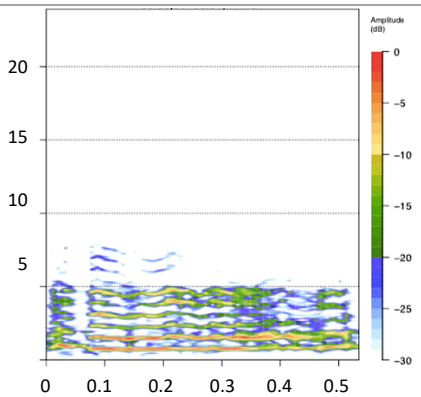
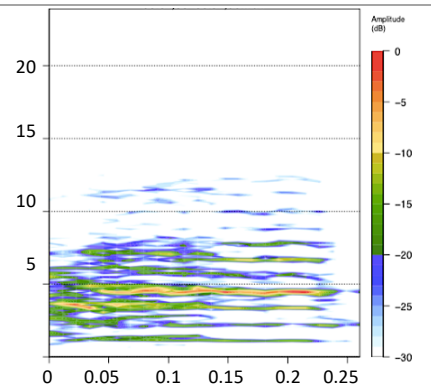
Behaviour category *Associated call type*	**Locomotion** -	
Behaviour *Call type*	**Climbing** *Very high pitched*	**Side-stepping** *Growl*
Rel. freq. of call type in behaviour	26.1%	21.1%
Mean no. pulses per call	1 ± 0	1.67 ± 1.2
Mean duration (ms)	261 ± 69	460 ± 9
Bandwidth (kHz)	6.727 ± 1.917	5.044 ± 0.908
Peak frequency (kHz)	3.881 ± 0.855	1.250 ± 0.423
Mean frequency (kHz)	6.499 ± 0.504	3.768 ± 0.445
Spectrogram (Frequency (kHz) / Time (s)) Coloured scale: rel. amplitude		

Behaviour category *Associated call type*	**Maintenance** *Growl*	
Behaviour *Call type*	**Preening** *Growl*	Spectrogram (Frequency (kHz) / Time (s)) Coloured scale: rel. amplitude
Rel. freq. of call type in behaviour	50.0%	
Mean no. pulses per call	1 ± 0	
Mean duration (ms)	626 ± 242	
Bandwidth (kHz)	6.128 ± 2.142	
Peak frequency (kHz)	1.906 ± 0.840	
Mean frequency (kHz)	4.684 ± 0.089	

Behaviour category *Associated call type*	**Sexual behaviour** *Mating, hiss*	
Behaviour *Call type*	**Attempted mounting** *Short*	Spectrogram (Frequency (kHz) / Time (s)) Coloured scale: rel. amplitude
Rel. freq. of call type in behaviour	100.0%	
Mean no. pulses per call	1.2 ± 0.4	
Mean duration (ms)	92 ± 57	
Bandwidth (kHz)	1.746 ± 0.718	
Peak frequency (kHz)	1.621 ± 0.470	
Mean frequency (kHz)	4.039 ± 0.483	
Behaviour *Call type*	**Hissing** *Hiss*	Spectrogram (Frequency (kHz) / Time (s)) Coloured scale: rel. amplitude
Rel. freq. of call type in behaviour	84.6%	
Behaviour *Call type*	**Mating** *Mating*	**Post-coital** *Mating*
Rel. freq. of call type in behaviour	96.3	40.0
Spectrogram (Frequency (kHz) / Time (s)) Coloured scale: rel. amplitude		

Behaviour category *Associated call type*	**Stationary** *Very high pitched, Pi*	
Behaviour *Call type*	**Hanging** *Very high pitched*	Spectrogram
Rel. freq. of call type in behaviour	21.35%	
Mean no. pulses per call	1.6 ± 0.9	
Mean duration (ms)	294 ± 81	
Bandwidth (kHz)	5.588 ± 1.651	
Peak frequency (kHz)	2.685 ± 0.877	
Mean frequency (kHz)	4.673 ± 1,051	
Behaviour *Call type*	**Perching** *Very high pitched*	*Pi*
Rel. freq. of call type in behaviour	24.1%	11.8%
Mean no. pulses per call	1.4 ± 1.1	1.8 ± 1.6
Mean duration (ms)	323 ± 86	360 ± 379
Bandwidth (kHz)	5.426 ± 1.899	6.603 ± 1.625
Peak frequency (kHz)	2.723 ± 0.680	2.988 ± 93
Mean frequency (kHz)	4.746 ± 1,008	5.456 ± 0.651
Spectrogram (Frequency (kHz) / Time (s)) Coloured scale: rel. amplitude		

Behaviour category *Associated call type*	**Vigilance** *Pip, Screech, High pitched*	
Behaviour *Call type*	**Alarm** *Pip*	**Alert** *High pitched*
Rel. freq. of call type in behaviour	39.6%	47.8%
Mean no. pulses per call	1.9 ± 1,0	1.1 ± 0.4
Mean duration (ms)	330 ± 177	279 ± 80
Bandwidth (kHz)	7.921 ± 0.710	4.894 ± 2.681
Peak frequency (kHz)	5.511 ± 1.42	2.519 ± 0.784
Mean frequency (kHz)	5.852 ± 0.510	4.733 ± 0.824
Spectrogram (Frequency (kHz) / Time (s)) Coloured scale: rel. amplitude		

Behaviour category *Associated call type*	**Other** *Peum, Annoyance*	
Behaviour *Call type*	**∩ -bob** *Peum*	**Head jerk** *Annoyance*
Rel. freq. of call type in behaviour	25.0%	60.0%
Mean no. pulses per call	1 ± 0	1 ± 0
Mean duration (ms)	324 ± 12	121 ± 22
Bandwidth (kHz)	7.548 ± 0.179	7.676 ± 1.712
Peak frequency (kHz)	2.934 ± 0.160	3.344 ± 1.172
Mean frequency (kHz)	4.303 ± 0.215	5.310 ± 0.666
Spectrogram (Frequency (kHz) / Time (s)) Coloured scale: rel. amplitude		
Behaviour *Call type*	**Neck stretching** *Parrot*	*Screech*
Rel. freq. of call type in behaviour	14.3%	28.6%
Mean no. pulses per call	1 ± 0	1 ± 0
Mean duration (ms)	313 ± 314	294 ± 47
Bandwidth (kHz)	4.795 ± 0.823	6.689 ± 0.037
Peak frequency (kHz)	1.475 ± 0.999	4.468 ± 0.008
Mean frequency (kHz)	3.787 ± 0.105	5.896 ± 0.132
Spectrogram (Frequency (kHz) / Time (s)) Coloured scale: rel. amplitude		

7.5 Photographs of each rainbow lorikeet of the Fugle Zoo population, with identifiable characteristics

Fig. 7.2. F1. Exhibits stress feather-picking; easily identified by having a completely naked breast and upper back, and a long deformed beak. Silver ring, left foot.

Fig. 7.3. M1. Permanently dirty tail feathers.

Fig. 7.4. F3. Worn-out red ring (pinkish), left foot.

Fig. 7.5. M3. Wide polished silver ring 18, left foot.

Fig. 7.6. F2. Electric-blue breast feathers. Silver ring 027 LDF, left foot.

Fig. 7.7. M2. Orange ring F75, right foot.

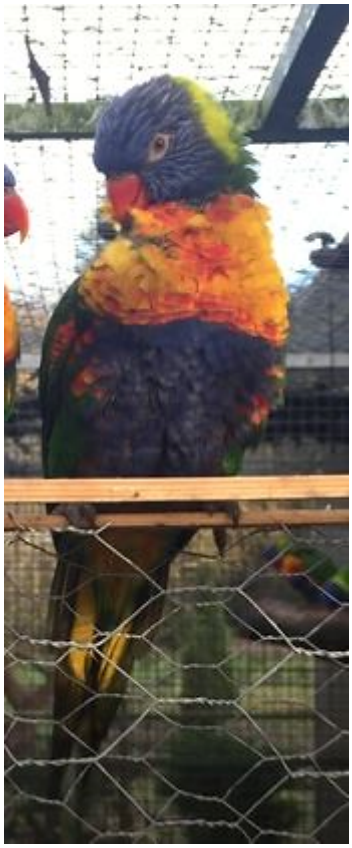


Fig. 7.8. F4. Silver ring 18, with red worn-out stripe.

Fig. 7.9. M4. First to alarm, frequently perched on the setup. Purple ring LDF 15 R 350, right foot.

Fig. 7.10. F5. Electric-blue breast feathers, permanently humid. Green ring, right foot.

Fig. 7.11. F6. Exhibits limping and right paw bulbous deformity, and identifiable behaviour. Silver ring LD1. 7.0, left foot.